

A review of the genus *Burnupena* Iredale, 1918 (Gastropoda: Buccinidae), with descriptions of two new species

by

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ABSTRACT

The southern African genus *Burnupena* Iredale, 1918, in the gastropod family Buccinidae has presented ongoing taxonomic problems because of morphological plasticity and the existence of forms that are intermediate between species. Based on morphological and genetic analyses, seven species can be recognised. In this paper we provide taxonomic descriptions of these species, including the merging of two previously recognised species as subspecies (*Burnupena cincta cincta* (Röding, 1798) and *B. cincta limbosa* (Lamarck, 1822)), and the recognition and description of two new species (*B. rotunda* and *B. denselirata*).

INTRODUCTION

Members of the genus *Burnupena* have had a complex taxonomic history, with most species described as *Buccinum* Linnaeus or *Purpura* Bruguière, and then transferred to *Cominella* Gray, before the genus *Burnupena* was erected by Iredale in 1918. Only three of the original specific names have been retained, namely, *papyracea* (Bruguière, 1789), *lagenaria* (Lamarck, 1822) and *limbosa* (Lamarck, 1822). The other species now have different names, because of homonymy or synonymy.

Notwithstanding two relatively recent revisions of the genus (Orr 1956; Barnard 1959), difficulties in identification remained, mainly due to the occurrence of phenotypic intermediates between sympatric forms (Kilburn 1972, Kilburn & Rippey 1982). Orr (1956) recognised only two species, *B. papyracea* and *B. delalandii* (Kiener, 1834) (now *B. catarrhacta* (Gmelin, 1791)). She also recognised four subspecies of *B. papyracea*, namely *B. p. papyracea* (Bruguière, 1789), *B. p. cincta* (Röding, 1798), *B. p. lagenaria* (Lamarck, 1822) and *B. p. tigrina* (Kiener, 1834 (now *B. pubescens* (Küster, 1858))). Barnard (1959) on the other hand, recognised six species, elevating Orr's four subspecies, as well as one of her synonyms of *B. papyracea*, namely *B. limbosa* (Lamarck, 1822), to specific level, although he noted that apart from the taxonomic status, there was little difference between his and Orr's conclusions.

Orr's and Barnard's differences of opinion about the *B. papyracea* complex were discussed by Kilburn (1972). He noted that 'the true position is a very complex one'. He considered that the most important factor is the distribution of the forms. Since the ranges of the forms overlap, they cannot, by definition, be treated as subspecies as recommended by Orr. Two alternatives suggested by Kilburn were that the forms could be regarded as ecomorphs, or as full species. Of the former alternative, Kilburn

notes that, whilst the forms do have fairly characteristic habitats, there is no obvious correlation between habitat and distribution patterns. Thus, regarding the forms simply as ecomorphs would 'generate more problems than it would solve'. With regard to the second alternative, Kilburn concedes that, whilst intermediates do occur, these are relatively rare, and that 'to lump all five taxa into one species would attribute to these hybrids an importance which in reality is quite unwarranted'. He concludes that some degree of reproductive isolation may be in progress, and that the most practical solution is to accord the forms full specific rank, at least until further study.

Based on morphometric and electrophoretic studies (Dempster 1995a), we consider that five of the species recognised by Barnard (1959) and Kilburn & Rippey (1982), namely *B. papyracea*, *B. pubescens*, *B. lagenaria*, *B. catarrhacta* and *B. cincta*, should be retained. However, the sixth species, *B. limbosa*, should be reduced to a subspecies of *B. cincta*. In addition, two new species, one of which has previously been confused with *B. papyracea*, are described. The object of this paper is to provide descriptions and diagnostic characters for these taxa.

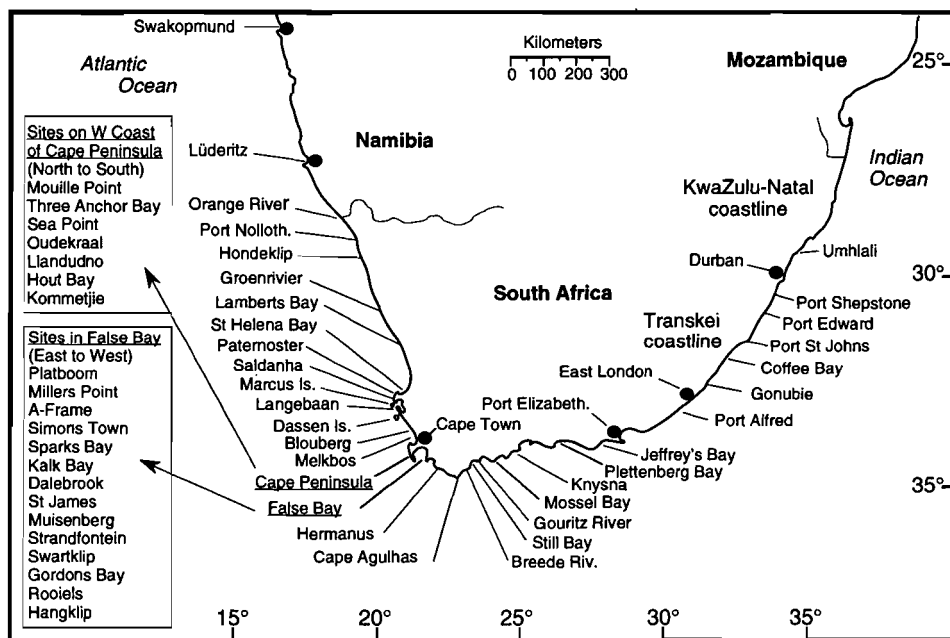


Fig. 1. Map showing localities mentioned in the text.

MATERIALS AND METHODS

The review of the genus is based on specimens collected by the authors for the morphometric and electrophoretic analyses (Dempster 1995a), as well as specimens from the following institutions: SAM, BMNH, MHNG, ANSP and MNHN (see abbreviations below). All localities mentioned in the text are shown in Fig 1.

Abbreviations used in the text are as follows:

ANSP – Academy of Natural Sciences, Philadelphia

BMNH	–	The Natural History Museum, London.
ICZN	–	International Commission on Zoological Nomenclature
MHNG	–	Museum National d'Histoire Naturelle, Geneva
MNHN	–	Museum National d'Histoire Naturelle, Paris
NM	–	Natal Museum, Pietermaritzburg
NMPG	–	Museum der Natur, Gotha
OXUM	–	Oxford University Museum
SAM	–	South African Museum, Cape Town
UCT	–	University of Cape Town ecological survey (deposited at SAM)
YD	–	specimens collected by first author or by members of Zoology Dept at UCT
ZMUC	–	Zoologisk Museum, Copenhagen

SYSTEMATICS

Key to the species and subspecies of *Burnupena*

- 1 Early whorls cancellate-nodulose (Fig. 37), though sometimes weakly so; live-collected specimens always covered with a bryozoan2
- Early whorls with spiral sculpture only (Fig. 36); live-collected specimens not covered with a bryozoan except in *B. papyracea*3
- 2 Shell with 10–14 spiral ribs on body whorl, often with nodules on shell other than on spire; shell often with flecked pattern (Figs 39–40).....
pubescens (Küster)
- Shell with numerous (usually > 14) weak spiral ridges on body whorl, never enlarged to ribs, with no nodules; spire only weakly cancellate; shell lacking axial flames or on early whorls only (Figs 45–46)**denselirata** sp. n.
- 3 Shell squat, spire obtuse; aperture length about twice spire length (e.g. Figs 15, 43)4
- Shell elongate, spire more acute, aperture length about equal to spire length (Fig. 5)5
- 4 Depression below suture moderate to strong (Figs 15–22); aperture usually smooth internally**lagenaria** (Lamarck)
- Slight to no depression below suture (see Fig. 43); aperture plicate internally
rotunda sp. n.
- 5 Profile of upper whorls distinctly convex (Figs 26, 30, 31); periostracum papery; colour relatively uniform, never flamed; live-collected specimens covered with a bryozoan**papyracea** (Bruguère)
- Profile of upper whorls only slightly or not convex; periostracum not papery; shell sometimes flamed; live specimens never with bryozoan6
- 6 Shell sculptured by 4 to 9 strong spiral ribs (see Figs 5–9)
cincta cincta (Röding)
- Shell with numerous spiral striae, never ribs (Figs 3, 13).....7
- 7 Aperture pale, plicate internally; shell uniformly brown or tinted green by algal

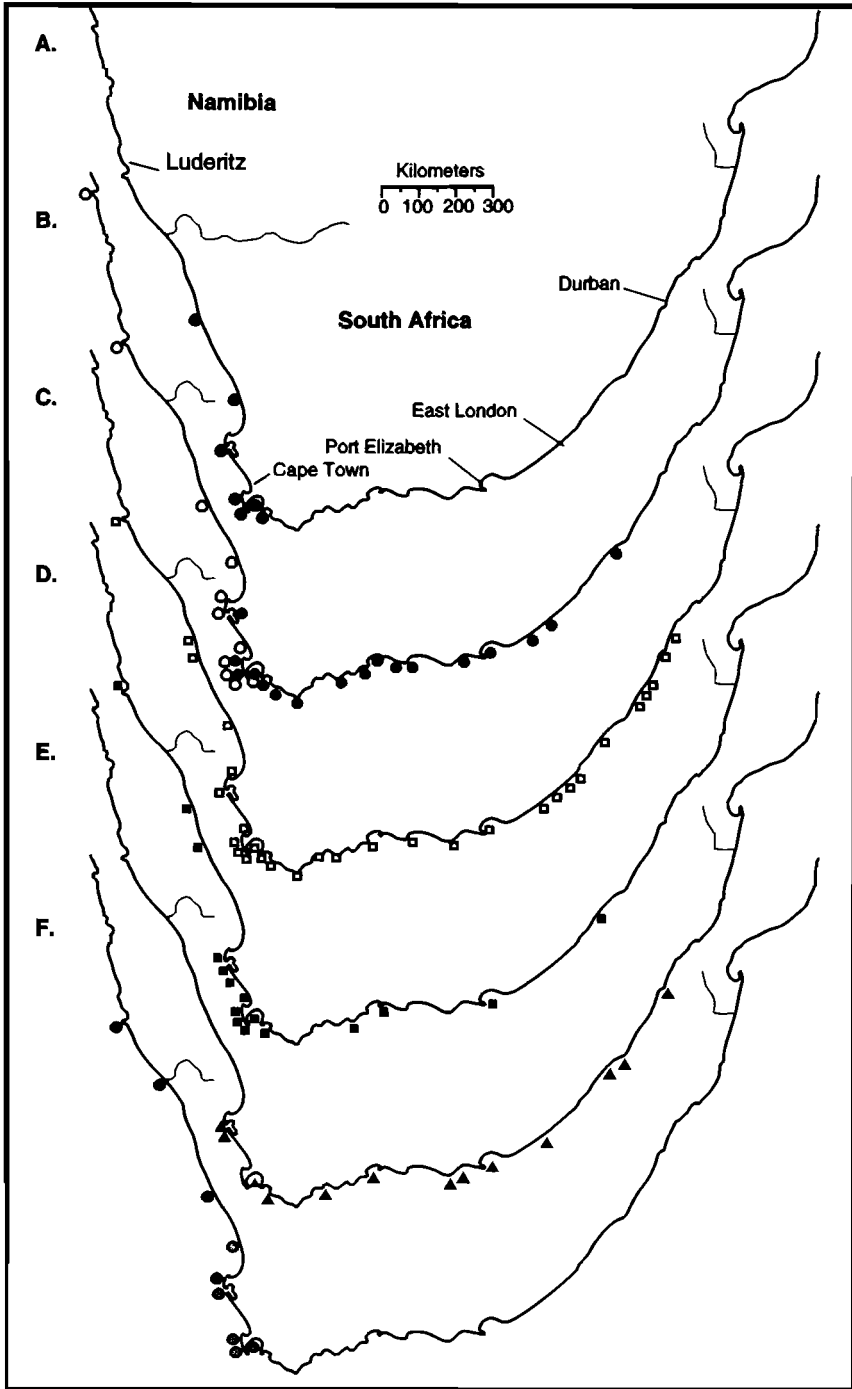


Fig. 2. Maps showing distribution of (a) *Burnupena catarrhacta*, (b) *B. cincta cincta* (black dots) and *B. cincta limbosa* (white circles), (c) *B. lagenaria*, (d) *B. papyracea*, (e) *B. pubescens*, (f) *B. rotunda*. Each dot represents one or more records. *B. denseliriata* is not shown as it has been recorded from False Bay only.

growth; periostracum thick, fibrous; proboscis flesh coloured (Figs 12–13).....

***cincta limbosa* (Lamarck)**

- Aperture dark, usually smooth internally; shell often with axial flames; periostracum thin; proboscis pigmented black (Fig. 3).....***catarrhacta* (Gmelin)**

Genus *Burnupena* Iredale, 1918

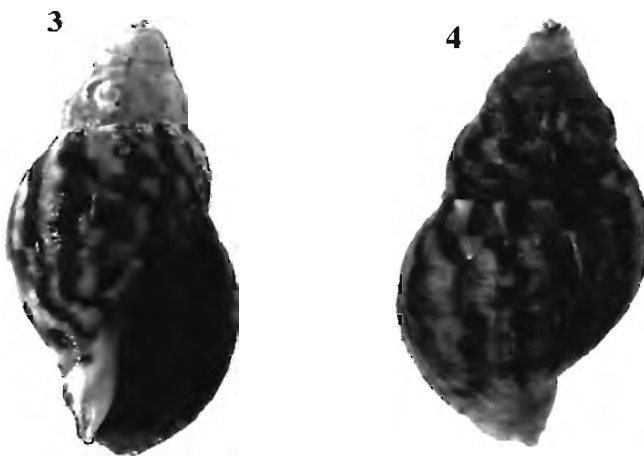
Burnupena Iredale, 1918: 28.

Type species: *Buccinum porcatum* Gmelin, 1791: 3494. (= *Buccinum cincta* Röding, 1798).

Diagnosis: Shell ovate, sometimes slightly fusiform, spire low to moderately high. Whorls more or less depressed below suture. Parietal callus dentiform. Canal short and wide. Fasciole distinct. Periostracum usually present. Spiral sculpture distinct, with early whorls sometimes cancellate. Radula with rectangular central plate armed with 4–9 small, peg-like denticles, laterals quadricuspid, cusps curved, outer cusp large, inner 3 cusps forming a group. Egg-capsules leaf-shaped, compressed, with apical flap, cemented to substrata in dome-shaped clusters.

Distribution: Endemic to Southern Africa, ranging from Namibia on the west coast to northern KwaZulu-Natal on the east coast.

Remarks: In the synonymies given below, the following two remarks are pertinent to most of the species. (1) Under the genus *Cominella*, Adams & Adams (1853) erected the subgenus *Amphissa* (into which they placed one of the members of *Burnupena*), but they listed the species of *Burnupena*, together with other species, under the genus *Cominella* without designating a subgenus, so in the following synonymies, the subgenus *Cominella* is inferred. (2) Stephenson (1948) referred to all of the species of *Burnupena* as *Cominella*, although he acknowledged that they fall under the 'section' *Burnupena*.



Figs 3–4. *Burnupena catarrhacta* from Kommetjie. Dimensions given for these and all other figures are shell lengths and widths: (3) 22.2 x 11.7 mm, (4) 22.9 x 12.3 mm.

Burnupena catarrhacta (Gmelin, 1791)

Figs 2a, 3–4

- Buccinum catarrhacta* Gmelin, 1791: 3498 (type figured in Chemnitz, 1788, pl. 152, fig. 1455).
Buccinum catarracta Dillwyn, 1817: 622.
Buccinum delalandii Kiener, 1834: 15, pl. 5, fig. 14; Deshayes, 1844: 189; Reeve, 1846, pl. 13, fig. 106.
 ?*Fusinus lineolatus* Dunker in Philippi, 1844 (non Costa, 1840): 110: pl. 1, fig. 10.
Buccinum catarracta Krauss, 1848: 119; 1852: 36.
Buccinum delalandi; Krauss, 1848: 120.
Cominella (Cominella) delalandii; Adams & Adams, 1853: 110.
 ?*Buccinum dunkeri* Küster, 1858: 86, pl. 15, figs 9–11 (substitute name for *lineolatus*).
 ?*Cominella dunkeri*; Kobelt, 1878: 232; Tryon, 1881: 203, pl. 80, figs 407–409; Sowerby, 1892: 10; Stephenson, 1948: 273.
Cominella delalandi; Kobelt, 1878: 232; Tryon, 1881: 203, pl. 80, fig. 413; Bartsch, 1915: 48; Odhner, 1923: 6.
Cominella catarracta; Kobelt, 1878: 232.
Cominella testudinea Bruguière, 1789; Tryon, 1881: 204, *partim*, pl. 80 (fig. 415 = *C. catarracta*, non fig. 414).
Cominella delalandii; Sowerby, 1892: 10; Cooke, 1917: 229, fig. 13 (radula); Turton, 1932: 52; Stephenson, 1948: 272.
Burnupena delalandii; Iredale, 1918: 34; Tomlin, 1926: 291; Barnard, 1959: 165; Kilburn, 1972: 415; Kensley, 1973: 152, fig. 551; Dance, 1974: 149; Day, 1974: 166, fig.; Richards, 1981: 60, pl. 32, fig. 262.
Burnupena delalandei; Peile, 1938: 97, fig. 31 (radula); Barnard, 1951: 69.
Burnupena delalandi; Orr, 1956: 258, pl. 19, fig. 10 (shell), pl. 20, fig. 1 (radula), text fig. 1f (radula).
Burnupena catarrhacta; Kilburn & Rippey, 1982: 94, pl. 21, fig. 10; Branch *et al.*, 1994: 162, fig. 76.3; Steyn & Lussi, 1998: 110, fig. 435.
Non Purpura catarracta Lamarck, 1822: 245; Kiener, 1834: 130, pl. 36, 37, figs 85, 85a–e; Deshayes, 1844: 81; Reeve, 1846, pl. 9, fig. 40; ?Sowerby, 1892: 14.

Diagnosis: Spire moderately long, angle usually 50–60°. Shell width approximately half shell length. Aperture slightly longer than spire. Periphery of body whorl situated approximately half way up shell. Sculptured by numerous fine spiral striae. Whorls slight to moderately depressed below suture; profile of upper whorls slightly convex. Outer lip thin, usually crenulated at margin, aperture sometimes (but not usually) plicate internally. Dark brown parietal scar usually present. Periostracum thin, yellowish-brown to brown. Shell sometimes with a yellowish-brown, sometimes greenish, ground colour, with well-defined dark brown axial flames, often giving a zigzag pattern, other times a spotted appearance – this coloration is most evident in juveniles; shell sometimes uniformly dark brown, other times worn. Aperture usually dark brownish-violet, often with a yellowish to whitish outer edge. Differs from all other *Burnupena* species in that the proboscis is coated with a black pigment. Maximum shell length 35 mm.

Distribution: West coast from Hondeklip southwards, and extending round to the south coast as far as Hermanus (Fig. 2a). Stephenson's (1948) record from Port Nolloth (north of Hondeklip) requires confirmation as he clearly confused this species with *B. lagenaria* (see remarks below). Tends to congregate in rock crevices, gullies and shallow pools at the mid- to high-tide level. Seldom abundant.

Material examined: Hondeklip (SAM A30969); Lamberts Bay (SAM A36381); Saldanha Bay (ANSP 196197); Langebaan Lagoon (UCT, YD); Oudekraal (SAM A30989, UCT); Kommetjie (SAM A51299, YD); Cape of Good Hope (MNHN – Kiener's syntypes of *Buccinum delalandii*); False Bay (SAM 11117); Simonstown (SAM 4751), Kalk Bay (SAM 2534, SAM 5513), Dalebrook (UCT, YD), Sparks Bay (YD) and Hangklip (SAM A30988).

Type material: *Buccinum catarrhacta* Gmelin 1791 – Gmelin referred to the specimen figured in Chemnitz (1788). The specimens from the latter collection are probably lost but may be in ZMUC (R. Kilburn, *pers. comm.*).

Buccinum delalandii Kiener, 1834 (MNHN): three syntypes; locality given as Cape of Good Hope.

Remarks: The earliest name given to this species was *Buccinum cataracta* by Chemnitz in 1788, and it was figured in his plate 152 (fig. 1455). However, the complete works of Martini and Chemnitz (1769 to 1795) were placed on the ‘Official List of Rejected Works in Zoology’ by the ICZN, under Opinion 184 of 1958, due to their use of polynomial names for many of the species. Subsequent authors proposed binomial names for Martini and Chemnitz’s figures (which have equal status as syntypes, R. Kilburn, *pers. comm.*) and sometimes used their names (or slight variations thereof), and thus took authorship.

In his synonymy of *Purpura cataracta*, Lamarck (1822) referred to the figures in Chemnitz and to Gmelin’s *Buccinum catarrhacta*, but he placed this species in the genus *Purpura*. However, from examination of photographs of his specimens, kindly made available by the MHNG, it is clear that these are not *Burnupena catarrhacta* or even a member of the genus. The spire is shorter, and the aperture larger than is typical for *Burnupena catarrhacta*, and they have axial ridges, a character state absent in *B. catarrhacta*. The locality given for Lamarck’s specimens was New Zealand. The same applies to Deshayes (1844), since he referred to Lamarck’s specimens. Reeve’s (1846) figure of *Purpura cataracta* is definitely not *B. catarrhacta*, but resembles *Nucella dubia* (Krauss). Kiener’s (1834) figures of *Purpura cataracta* resemble those of Lamarck’s specimens. Sowerby gave no figures, but referred to Reeve’s *Purpura cataracta*. Tryon (1881) regarded *Cominella cataracta* (fig. 415), which is the same as the specimen figured by Chemnitz (1788, pl. 152, fig. 1455) as a colour variation of *Cominella testudinea* (Bruguère), but the latter is a New Zealand species which is synonymous with *Cominella maculosa* (Marty, 1784). Thus it is clear that *Purpura cataracta* is unrelated to the South African material, for which the earliest valid name is *Buccinum catarrhacta*.

We have provisionally placed *Buccinum dunkeri* (and other combinations of Küster’s name), in synonymy, because Kuster’s figures clearly show a flame-like axial pattern and only a slight concavity below the suture. Its position is, however, uncertain. Kuster’s name was proposed as a substitute for *Fusus lineolatus* Dunker in Phillipi, 1844 (non Costa, 1840), but Phillipi’s figures do not resemble any known species of *Burnupena*. Tryon (1881) remarked that *B. dunkeri* is a doubtful species, and even its pertinence to the genus (*Cominella*) is problematical. However, both Orr (1956) and Barnard (1959) synonymised it with *Burnupena cincta*. The radula figured by Peile (1938) is that of a juvenile, and he noted that this species can be placed in *Burnupena* based on the lateral teeth, although the central plate (rhachidian) does resemble that of *Afrocominella* Iredale.

There has been much confusion in the literature and museum collections between *B. catarrhacta* and *B. limbosa*, and between *catarrhacta* and the new species described below as *B. rotunda*, and west coast specimens of *B. lagenaria*. The *B. delalandii* sample in the reference collection from the UCT ecological survey,

identified by Barnard in 1947 (SAM A36381 – locality Lamberts Bay), consists of four specimens. Two of these are *B. lagenaria*, one is *B. catarrhacta*, and the fourth is very small and its identity uncertain. Two samples of *B. delalandii* from Lüderitz (SAM A30521 and SAM A30530) comprise specimens of *B. rotunda*, whilst two others from the same locality (SAM A33404 and SAM A3306) are *B. lagenaria*. In a series of papers on the South African intertidal zones, Bright (1938) noted that *Cominella delalandii* was ‘almost ubiquitous in damp places’ at Port Nolloth, and Stephenson *et al.* (1940) referred to the ‘small black whelk *C. delalandii*’ as common at Lamberts Bay. Although we did not sample at Lamberts Bay, no *B. catarrhacta* were found at Port Nolloth, nor at Groen River, a site between Port Nolloth and Lamberts Bay. *B. lagenaria* was, however, very common at both sites. We believe that the specimens identified as *C. delalandii* by Bright (1938) and Stephenson (1940) were in fact *B. lagenaria*.

Burnupena catarrhacta can usually be distinguished from *B. lagenaria* by its more slender shape, longer spire and lack of spiral ridges, and by its black pigmented proboscis. When present, the pattern of axial flames is usually a good identifying character state for *B. catarrhacta*. However, certain populations of *B. lagenaria* (especially those on the west coast) can be confused with *B. catarrhacta*, because they lack spiral ridges and possess an axial pattern. In such cases however, the longer spire of *B. catarrhacta* usually distinguishes this species. Nevertheless, problems in identification do occur at some localities, for example Kommetjie, where members of the *B. lagenaria* population tend to have relatively longer spires.

Barnard (1959) commented on a ‘subscalariform’ specimen collected in False Bay (SAM 11117), which he identified as *B. lagenaria*. However, an inspection shows the specimen is a normal, although relatively high-spired, example of *B. catarrhacta*.

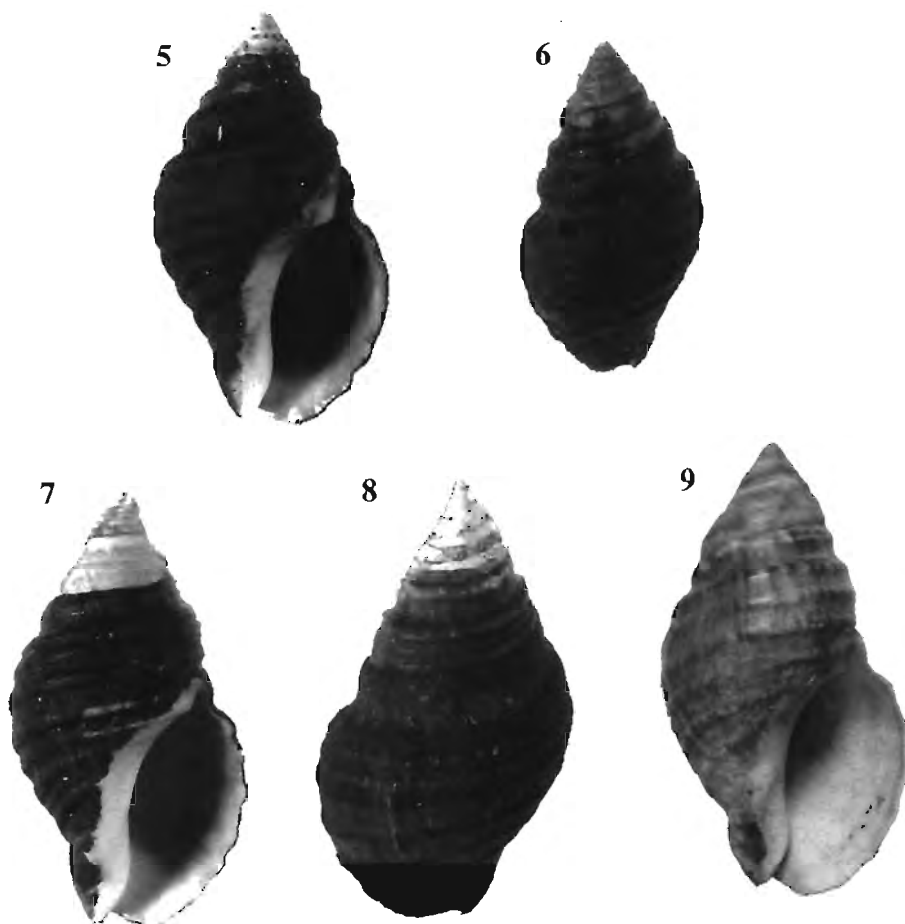
Barnard (1959) commented that ‘there are no clear-cut conchological differences between this species [*B. catarrhacta*] and *limbosa*’, but that ‘fresh specimens may be separated by colouration’. The two species can however, usually be distinguished. Large specimens of *B. cincta limbosa* can be separated by their larger size. Where size cannot be used, *B. catarrhacta* can usually be distinguished by its more acute spire, the dark colour of the aperture, and by the pattern of axial flames. Since there has been much confusion between *B. catarrhacta* and *B. lagenaria*, we suspect that many of the problems experienced by Barnard (1959) in distinguishing between *B. catarrhacta* and *B. limbosa*, were rather a matter of distinguishing between *B. lagenaria* and *B. limbosa*.

Burnupena catarrhacta can be distinguished from *B. rotunda* by its totally different shape, being slender and high spired, whilst *B. rotunda* is typically short and squat.

Burnupena cincta cincta (Röding, 1798)

Figs 2b, 5–11

- Buccinum mexicanum* Bruguière, 1789: 260 (types figured in Chemnitz 1780, pl. 126, figs 1213, 1214).
Buccinum porcatum (non da Costa, 1778) Gmelin, 1791: 3494; Dillwyn, 1817: 635; Deshayes, 1844: 190; Reeve, 1846, pl. 4, fig. 22; Krauss, 1848: 119; Küster, 1858: 82, pl. 14, fig. 14.
Buccinum cinctum Röding, 1798: 113.
Purpura ligata Lamarck, 1822: 244.
Buccinum ligatum; Kiener, 1834: 7, pl. 5, fig. 15.
Cominella ligata; Gray, 1850: 72; 1857: 15.



Figs 5–9. *Burnupena cincta cincta* from: (5) Port Elizabeth, 50.4 x 27.7 mm, (6) Port Elizabeth, 43.3 x 23.1 mm, (7) Dalebrook 44.1 x 23.3 mm, (8) Plettenberg Bay 44.4 x 26.1 mm (ANSP 196292), (9) Type specimen of *Buccinum ligatum* Lamarck, 1822, 56.0 x 29.5 mm (MHNG 1152/46: potential lectotype).

Buccinum crassum Mörch, 1852 (non Nyst, 1845): 94.

Purpura zeyheri Krauss, 1852: 35; Sowerby, 1892: 14.

Buccinum zeyheri; Küster, 1858: 85, pl. 15, figs 6–8.

Cominella semisulcata Sowerby, 1892: 10, pl. 1, fig. 7.

Cominella porcata; Kobelt, 1878: 231; Tryon, 1881: 202, *partim*, pl. 80 (figs 392, 393 = *C. ligata*, non figs 394, 395, 396, 399, 404); Sowerby, 1892: 10; Bartsch, 1915: 47; Cooke, 1917: 229, fig. 16 (radula).

Cominella zeyheri; Kobelt, 1878: 232; Tryon, 1881: 203, pl. 80, figs 405–406.

Burnupena cincta; Iredale, 1918: 34; Tomlin, 1926: 291; Peile, 1938: 97; Barnard, 1951: 69, pl. 7, figs 2–3, text fig. 35 (egg capsule); 1959: 160, figs 31g (radula), 32a–e (shell and protoconch); Kilburn, 1972: 415; Dance, 1974: 149, fig.; Day, 1974: 166, fig.; Kilburn & Rippey, 1982: 94, pl. 21, figs 9a–b; Branch *et al.*, 1994: 162, fig. 76.1; Steyn & Lussi, 1988: 108, fig. 430.

Burnupena (Burnupena) porcata; Thiele, 1929: 315.

Cominella translucida Turton, 1932: 51, pl. 12, fig. 379.

Cominella cincta; Turton, 1932: 51; Stephenson, 1948: 272; Bokenham & Neugebauer, 1938: 133, pl. 16, figs 1–3, 5–6, 9.

Cominella cincta adjacens Turton, 1932: 52, pl. 12, fig. 381.

?*Burnupena dunkeri*; Peile, 1938: 98, fig. 33 (radula).

Burnupena papyracea cincta; Orr, 1956: 254, pl. 19, figs 5–6 (shell), pl. 20, fig. 2 (radula), text figs 1b–c (radula); Kensley, 1973: 152, fig. 552; Richards, 1981: 60, pl. 32, fig. 263.

Diagnosis: Spire moderately high, angle usually 60–70°. Shell width approximately half shell length. Aperture slightly longer than spire. Periphery of body whorl situated approximately half way up shell. Sculptured, usually by strong spiral ribs, occasionally weaker, with fine spiral striae on and between ribs. Typically between 4 and 9 spiral ribs on body whorl. Whorls moderately to strongly depressed below suture; profile of upper whorls stepped to straight. Shell robust. Outer lip undulate at margin (corresponding to ribs), sometimes crenulated at edge; aperture usually smooth internally, sometimes plicate. Pale brown parietal scar usually present. Periostracum thick, fibrous, brown, sometimes stained with green algae. Shell colour usually dull dark brown, occasionally with alternating dark brown and pale whitish-brown dashes on a few of the main spiral ribs; shell sometimes worn or colour completely obscured by periostracum or by algal growth. Aperture light mauve-brown to pale violet, occasionally white. Proboscis flesh coloured. Maximum shell length 64 mm.

Distribution: False Bay to Transkei on the South Coast, and sporadically on the west coast as far as Saldanha Bay (Fig. 2b).

Material examined: Saldanha Bay (SAM A4738, ANSP 196198); Sea Point (SAM 2542, SAM A4737); Kommetjie (SAM A51301); False Bay: Castle Rock (YD), A-Frame (YD), Kalk Bay (SAM 6545), Dalebrook (YD), St. James (SAM A49960), Muizenberg (SAM A51886), Zwartklip (SAM A8605), Gordon's Bay (ANSP 196206), Sparks Bay (YD), Rooiels (YD) and Pringle Bay (YD); Onrus (ANSP 196205); Hermanus (ANSP 196202, ANSP 196203, ANSP 196204); Cape Agulhas (ANSP 196296); Still Bay (SAM A30967, SAM A30974); Gouritz River mouth (ANSP 196295); Mossel Bay (SAM 2436, SAM A49959, ANSP 196293, ANSP 196294, YD); Knysna (SAM A4739); Plettenberg Bay (ANSP 196290, ANSP 196292); Jeffrey's Bay (SAM A30966, SAM A49965, ANSP 196297); Port Elizabeth (SAM A4740, YD); East London (SAM A36380); Gonubie (SAM A39271); Qolora (UCT); Port St. Johns (SAM 2507, SAM 11353).

Type material: *Buccinum cinctum* Röding, 1798: type presumed lost (R. Kilburn, pers. comm.); Röding referred to the specimen figured in Chemnitz 1780, but the specimens from the latter collection are lost. Syntypes possibly in NMPG (Bolten Colln) or ZMUC (Chemnitz colln) (R. Kilburn, pers. comm.).

Purpura ligata Lamarck, 1822 (MHNG 1152/46 – photographs seen): three specimens, one of which is a potential lectotype (Fig. 9) as it matches the size and illustration of *Buccinum ligatum* given by Kiener (1834, pl. 15, fig. 15); no locality given.

Buccinum crassum Mörch, 1852: type probably lost.

Cominella semisulcata Sowerby, 1892: holotype BMNH 99.4.14.3679.

Cominella cincta adjacens Turton, 1931: syntype in OXUM.

Remarks: The earliest name given to this species was *Buccinum asperius striatum* by Chemnitz in 1780, and figured in his plate 126 (figs 1213, 1214). However, as noted

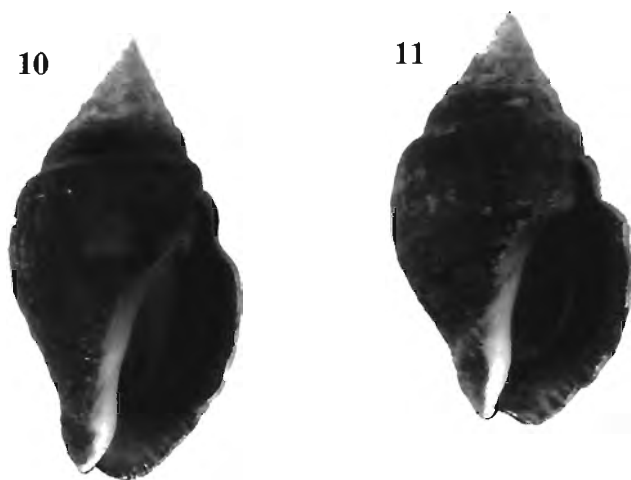
above, Chemnitz's names are invalid, although the figures are frequently cited and are regarded as the type figures.

Buccinum mexicanum, proposed by Bruguière in 1789, is the oldest available name for this species, but it has not been used since, and has only been listed as a synonym (e.g. Dillwyn 1817; Reeve 1846) in some of the older works. On the other hand, the name *cincta* has been used in at least 25 publications by more than 10 authors in the past 50 years. An application for *mexicanum* to be placed on the Official Index of Rejected and Invalid Specific Names in Zoology, and that of *cincta* to be placed on the Official List of Specific Names in Zoology, has been submitted to the ICZN (Dempster 1995b). The ICZN has responded that there are impending changes to the code, and under Article 23.9 of the new Code (due to come into effect on 1 January 2000), *cincta* will permanently take precedence over *mexicanum*.

Under Lamarck's *Purpura ligata*, Deshayes (1844) commented that, in agreement with Kiener, this was a *Buccinum*, not a *Purpura*, but he also noted that it is the same as Gmelin's *Buccinum porcatum*.

Thiele (1929) regarded the two genera erected by Iredale (1918), namely *Afrocominella* and *Burnupena*, as sections or subgenera of *Burnupena*, although he should have named *Afrocominella* as the genus as it has line precedence.

Both Orr and Barnard regarded *Cominella translucida* Turton, 1932, as a synonym of *Burnupena tigrina* (= *B. pubescens*). However, the number of spiral ribs on the last whorl (about 7), together with the lack of nodules on the spire (although these could have been worn off as the specimen is clearly worn), make it more likely that this was based on a specimen of *B. cincta*.



Figs 10–11. *Burnupena cincta cincta*, 33.4 x 17.3 mm (10) and *B. lagenaria*, 31.4 x 17.6 mm (11), both from Mossel Bay, showing the similarities between intermediate forms of the two species.

Burnupena cincta cincta is common from the mid-intertidal to the shallow subtidal zone, and is not usually found in exposed positions. In its typical form, there is usually no difficulty in its identification. However, it can be confused with both *B.*

lagenaria and *B. cincta limbosa*. Barnard (1959) regarded *B. c. cincta* and *B. lagenaria* as one of the 'two most confusing pairs'. The two taxa often co-occur, although *B. lagenaria* is generally found higher up the shore, and in more exposed positions. The extreme forms are distinctive, with specimens of *B. c. cincta* having relatively longer spires and strong spiral ribs, whilst those of *B. lagenaria* have short spires and weak ribs. The problem is that phenotypic intermediates are not uncommon (Figs 10–11), with specimens of *B. lagenaria* with longer spires and strong ribs apparently more common than specimens of *B. c. cincta* with squat shells and weak ribs (pers. observation). However, they can usually, but not always, be distinguished by the colour of the aperture and of the shell. In *B. c. cincta* the aperture is pale to violet, whilst that of *B. lagenaria* is typically dark. The shell colour of *B. c. cincta* is usually brown and only occasionally flecked, whilst that of *B. lagenaria* is often flecked or flamed, but sometimes is only brown.

Burnupena c. cincta has been confused with *B. c. limbosa* as they are very similar in most respects, although they differ in the degree of spiral ribs; individuals of the former usually have strong ribs, whilst individuals of *B. c. limbosa* either have smooth shells or a few weak ribs on the lower half of the body whorl. We consider that *limbosa* should be reduced to a subspecies of *B. cincta*, but see remarks below.

Burnupena cincta limbosa (Lamarck, 1822)

Figs 2b, 12–14

Purpura limbosa Lamarck, 1822: 243; *non* Kiener, 1834: 127, pl. 40, fig. 95; Deshayes, 1844: 78.

Buccinum limbosum; Reeve, 1846, pl. 5, fig. 35; Krauss, 1848: 119; 1852: 35; Küster, 1858: 74, pl. 13, fig. 10.

Cominella limbosa; Gray, 1850: 72; 1857: 15; Kobelt, 1878: 231; Tryon, 1881: 202, *partim*, pl. 80, fig. 397, *non* figs 398, 400, 403; Sowerby, 1892: 10; Bartsch, 1915: 48; Cooke, 1917: 229, fig. 15 (*radula*); Tomlin, 1922: 260; Odhner, 1923: 6; Stephenson, 1948: 273.

Cominella (Cominella) limbosa; Adams & Adams, 1853: 110, pl. 11, fig. 6c.

Buccinum (Cominella) limbosa; Chenu, 1859: 158, fig. 739.

Cominella porcata multilirata Bartsch, 1915: 47, pl. 4, fig. 6.

Burnupena limbosa; Iredale, 1918: 34; Tomlin, 1926: 291; Peile, 1938: 97; 1939: 270, fig. 38 (*radula*); Barnard, 1951: 69, pl. 7, fig. 4; 1959: 164; Kilburn, 1972: 415; Dance, 1974: 149, fig.; Day, 1974: 166, fig.; Kilburn & Rippey, 1982: 94, pl. 21, fig. 12; Steyn & Lussi, 1998: 110, fig. 432.

Cominella cincta multilirata; Turton, 1932: 52.

Cominella lagenaria limbosa; Turton, 1932: 52.

Burnupena papyracea papyracea (non Bruguière); Orr, 1956: 252, *partim*, pl. 19, fig. 1, *non* figs 2–4.

Diagnosis: Spire moderately high, angle usually 60–80°. Shell width slightly more than half shell length. Aperture slightly longer than spire. Periphery of body whorl situated approximately half way up shell. Sculptured usually by numerous fine spiral striae, sometimes with a few weak ribs on lower half of body whorl. Whorls slight to moderately depressed below suture; profile of upper whorls slightly convex. Shell robust. Aperture usually plicate internally. Pale brown parietal scar usually present. Periostracum thick, fibrous, brown. Shell colour uniformly dark brown, sometimes with thin pale whitish-brown spiral bands, these being most noticeable on the body whorl above parietal region; shell sometimes worn or colour completely obscured by greenish algal growth. Aperture white to light mauve-brown, sometimes with a darker brownish-violet outer edge. Proboscis flesh coloured. Maximum shell length 60 mm.

Distribution: West coast from Swakopmund southwards, and extending around Cape Point to Simonstown (Fig. 2b), with two questionable records at Jeffrey's Bay and Gonubie.

Material examined: Swakopmund (SAM A29892, YD); Lüderitz (YD); Lamberts Bay (SAM A30986); Paternoster (UCT, YD); Marcus Island (YD); Melkbos (SAM A49957); Blouberg (YD); Table Bay (SAM 5469); Sea Point (UCT, ANSP 196301, BMNH 2258); Oudekraal (UCT, YD); Hout Bay (SAM A4745); Kommetjie (SAM A49956, YD); Cape of Good Hope (BMNH 1840.9.20.26, BMNH 1876.5.19.4); Simonstown (SAM 4748).



Figs 12–14. *Burnupena cincta limbosa* from Bakoven: (12) 50.4 x 28.4 mm; (13) 50.0 x 28.5 mm; and (14) Type specimen of *Purpura limbosa* Lamarck, 1822, 35.5 x 20.6 mm (MHNG 1101/60/1: syntype).

Type material: *Purpura limbosa* Lamarck 1822 (MHNG 1101/60 – photographs seen): two syntypes, one of which is shown in Fig. 14; no locality given. *Cominella porcata multilirata* Bartsch, 1915: holotype USNM 16986.

Remarks: Kiener's (1834) *Purpura limbosa* is clearly not this species, but is a specimen of *B. lagenaria*. Tryon (1881) commented that *Cominella limbosa* might prove to be a well-marked variety of *C. porcata* (i.e. *B. cincta*), an opinion that is substantiated herein.

Burnupena cincta limbosa inhabits the low intertidal to subtidal zone. We have reduced it to a subspecies of *B. cincta* based on the combined results of morphometric and electrophoretic studies (Dempster 1995a), together with the fact that *limbosa* and *cincta* occupy different geographic regions. The two taxa are very similar genetically, and differ morphometrically only in the extent of spiral ribbing present: *B. cincta cincta* is typically strongly ribbed, whilst *B. cincta limbosa* is typically smooth shelled. This distinction allows for relatively easy separation.

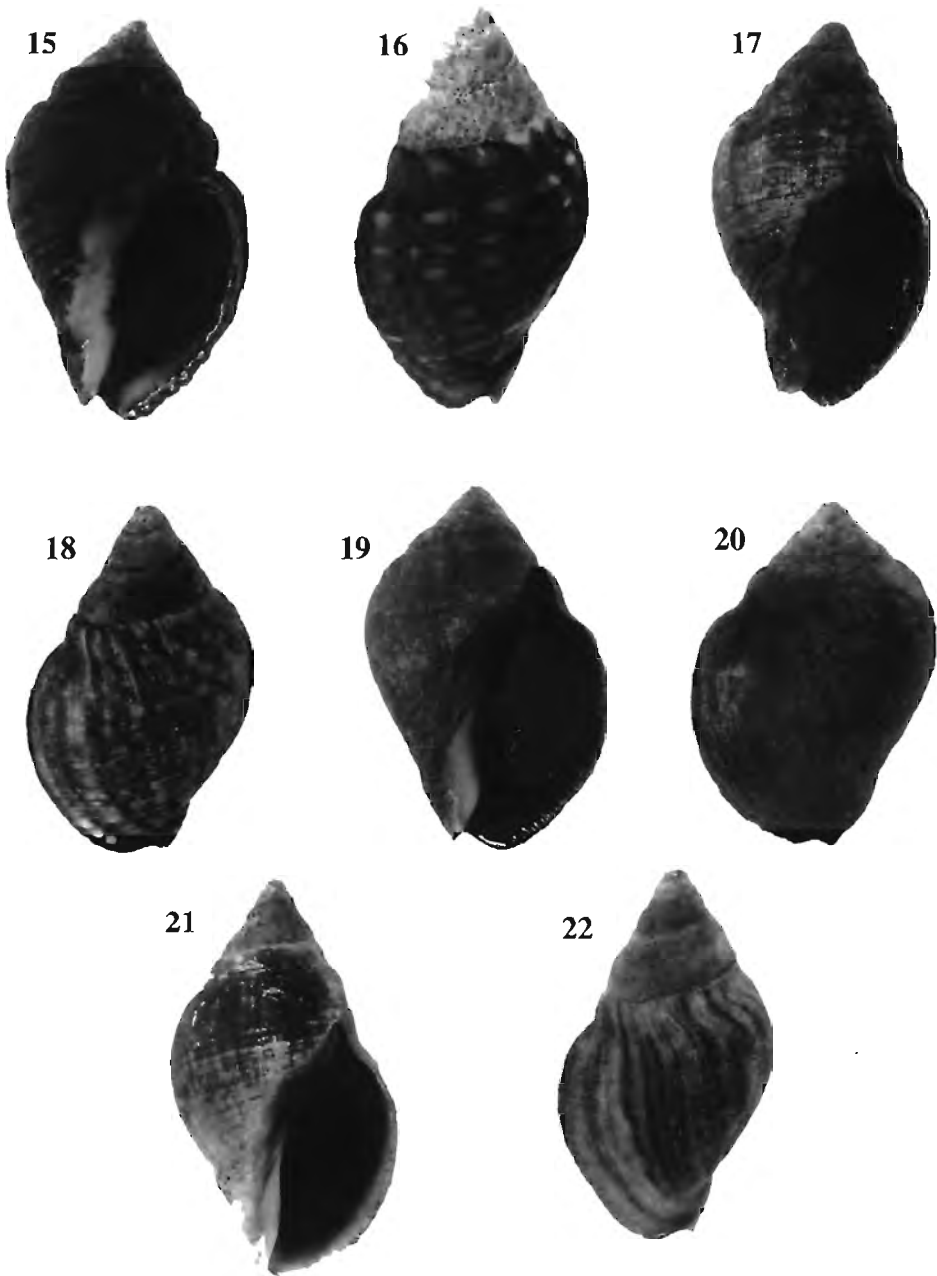
Burnupena c. limbosa has, however, been confused with a number of other species of *Burnupena*. Barnard (1959) regarded this taxon and *B. catarrhacta* as one of the 'two most confusing pairs'. The distinctions between them have been discussed in the remarks on *B. catarrhacta*. However, as noted above, Barnard seems to have confused *B. catarrhacta* and *B. lagenaria*. Of a total of 23 specimens from the BMNH which had been identified as *B. limbosa*, 12 are specimens of *B. lagenaria*. The two species can usually be distinguished by: (1) the height of the spire, with *B. lagenaria* generally having the shorter spire; (2) whether or not the aperture is plicate internally, with *B. c. limbosa* almost always plicate, but *B. lagenaria* usually not plicate, and (3) the colour of the shell and the aperture – *B. c. limbosa* with a brown shell and pale aperture, *B. lagenaria* with a flecked or brown shell and dark aperture. About one-third of the specimens at SAM identified as *B. limbosa* were not this species, and of these approximately half are specimens of *B. rotunda*. However, *B. c. limbosa* can be usually be distinguished from *B. rotunda* by (1) the height of the spire, which is shorter in *B. rotunda*, (2) the length of the aperture, which is about twice the length of the spire in *B. rotunda*, but only slightly longer than the spire in *B. c. limbosa*, (3) the shell colour – dark brown in *B. c. limbosa*, but bluish-brown in *B. rotunda*, and (4) in certain populations, the colour of the aperture – always pale in *B. c. limbosa*, but dark in some populations of *B. rotunda*.

Burnupena lagenaria (Lamarck, 1822)

Figs 2c, 15–24

- Purpura lagenaria* Lamarck, 1822: 245; *non* Duclos, 1832: 112, pl. 2, fig. 11; Kiener, 1834: 128, *partim*, pl. 40, fig. 94, *non* figs 94a, 94b; Deshayes, 1844: 81.
- Purpura cucurbita* Duclos, 1832: 112, pl. 2, fig. 12.
- Buccinum violaceum* Quoy & Gaimard, 1832: 456, pl. 30, figs 32–34; Kiener, 1834: 33, pl. 8, fig. 23; Krauss, 1848: 120.
- Purpura limbosa* (*non* Lamarck) Kiener, 1834: 127, pl. 40, fig. 95.
- Buccinum lagenarium*; Reeve, 1846, pl. 5, figs 33–34; Krauss, 1848: 119; Küster, 1858: 82, pl. 14, figs 15–16, pl. 15, figs 1–2.
- Cominella lagenaria*; Gray, 1850: 72; 1857: 15; Kobelt, 1878: 231; Sowerby, 1892: 10; Bartsch, 1915: 48; Cooke, 1917: 229, fig. 14 (radula); Tomlin, 1922: 260; Turton, 1932: 52; Stephenson, 1948: 272.
- Cominella* (*Cominella*) *lagenaria*; Adams & Adams, 1853: 110.
- Buccinum* (*Cominella*) *lagenaria*; Chenu, 1859: 158, fig. 738.
- Cominella violacea*; Kobelt, 1878: 232; Tryon, 1881: 203, pl. 80, figs 410–412; Sowerby, 1892: 10.
- Cominella limbosa*; Tryon, 1881: 202, *partim*, pl. 80, fig. 398, *non* fig. 397.
- Cominella limbosa* var. *lagenaria*; Tryon, 1881: 202, pl. 80, figs 400, 403.
- Burnupena lagenaria*; Iredale, 1918: 34; Tomlin, 1926: 291; Peile, 1938: 97; Barnard, 1951: 69, pl. 7, fig. 5; 1959: 162; Kilburn, 1972: 415; Dance, 1974: 149, fig.; Day, 1974: 166, fig.; Kilburn & Rippey, 1982: 94, pl. 21, fig. 13, text fig. 54 (egg capsule); Lasiak & van der Horst, 1988: 128 on, text fig. 4 (egg capsules); Branch *et al.*, 1994: 162, fig. 76.2; Steyn & Lussi, 1998: 108, fig. 431.
- Burnupena* (*Burnupena*) *lagenaria*; Thiele, 1929: 315, fig. 349 (radula).
- Burnupena papyracea papyracea* (*non* Bruguière); Orr, 1956: 252, *partim*, pl. 19, fig. 3, *non* figs 1–2, 4 (shell).
- Burnupena papyracea lagenaria*; Orr, 1956: 256, pl. 19, fig. 9 – shell, text fig. 1g,h (radula); Kensley, 1973: 152, fig. 553; Richards, 1981: 60, pl. 32, fig. 264.

Diagnosis: Shell squat with low spire, angle usually 70–80°. Shell width more than half shell length. Aperture approximately twice as long as spire. Periphery of body whorl situated slightly closer to apex. Sculpture usually in the form of weak spiral



Figs 15–22. *Burnupena lagenaria* from (15) Port Elizabeth: 29.8 x 19.1 mm, (16) Dalebrook: 31.8 x 17.9 mm, (17) Groen River: 34.3 x 20.1 mm and (18) 32.3 x 19.8 mm, (19) Durban: 23.5 x 15.4 mm and (20) 23.2 x 16.1 mm, (21) Kommetjie: 28.1 x 15.8 mm and (22) 27.5 x 15.3 mm.

ribs with fine spiral striae on and between ribs, sometimes with spiral striae and a few weak ribs on lower half of body whorl. Typically between 4 and 9 spiral ribs on body whorl. Whorls moderately to strongly depressed below suture; profile of upper whorls stepped to straight. Outer lip usually crenulated at edge, aperture smooth internally, sometimes plicate. Dark brown parietal scar usually present. Periostracum thick, fibrous, brown, often stained with green algae. Shell colour often with yellowish-brown to brown ground colour, with well-defined alternating dark brown and pale whitish-brown to yellowish dashes on main spiral ribs, sometimes giving a wavy axially flamed appearance; the dashes on the spiral ribs are usually present over most of the body whorl, and are most prominent just below the suture and on the shoulder of the body whorl; sometimes the alternating dashes are not well defined, giving the shell a streaky appearance; shell colour sometimes dark brown, completely lacking the alternating dark and light dashes; upper whorls of shell usually worn. Aperture usually dark brownish-violet, or yellowish-violet, often with a yellowish to whitish outer edge. Proboscis flesh coloured. Maximum shell length 45 mm.

Distribution: From Lüderitz (in Namibia) on the west coast, extending to northern KwaZulu-Natal on the east coast (Fig. 2c).

Material examined: Lüderitz (SAM A3306, SAM A33404); Hondeklip (SAM A30969); Groen River (YD); Lamberts Bay (SAM A36381); St. Helena Bay (SAM A49958, UCT); Saldanha Bay (ANSP 196197); Langebaan Lagoon (SAM A30971, UCT, YD); Melkbos (SAM A39292); Blouberg (SAM A38155, YD); Table Bay (SAM 5470, MNHN – syntype of *Buccinum violaceum*); Sea Point (SAM A4737, ANSP 196301, ANSP 196302, BMNH 2258); Mouille Point (SAM A51298); Kommetjie (YD); Platboom (ANSP 196300); Cape of Good Hope (BMNH 1822); False Bay: Simonstown (ANSP 196200), Kalk Bay (SAM A4741), Dalebrook (YD), Zwartklip (SAM A8606), Gordon's Bay (ANSP 196206), Sparks Bay (YD), Cape Hangklip (SAM A51302); Onrus (ANSP 196205); Hermanus (ANSP 196201, ANSP 196202, YD); Cape Agulhas (ANSP 196296); Breede River estuary (UCT); Still Bay (SAM A30974); Mossel Bay (SAM 2436, ANSP 196293, YD); Plettenberg Bay (ANSP 196290, ANSP 196291, ANSP 196292); Jeffrey's Bay (ANSP 196297, UCT); Port Elizabeth (SAM A36382, ANSP 196289); Richmond (UCT); Kleinmond (UCT); East London (SAM A4742, ANSP 196287, ANSP 196289); Gonubie (SAM A51405); Qolora (SAM A30987, UCT); Coffee Bay (SAM A49961); Mbotyi (SAM A49962); Port Edward (UCT); Port Shepstone (SAM A30061); Durban (YD); Umhlali (SAM A30972).

Type material: *Purpura lagenaria* Lamarck, 1822 (MHNG 1101/64 – photographs seen): three syntypes, one of which is shown in Fig. 23; no locality given.

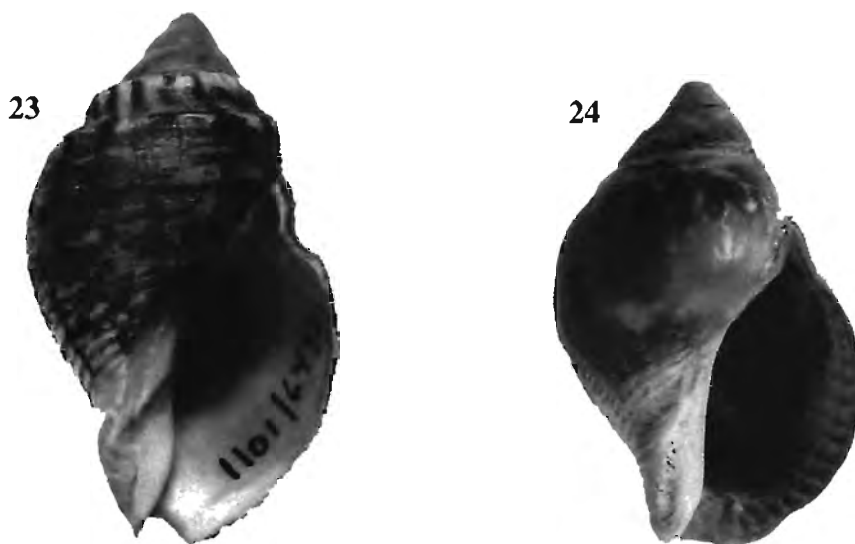
Purpura cucurbita Duclos, 1832: possibly in MNHN.

Buccinum violacea Quoy & Gaimard, 1832: syntype in MNHN.

Remarks: Duclos's (1832) *Purpura lagenaria* is not this species, but resembles *Nucella dubia*. However, he also introduced a new name, *Purpura cucurbita*, the description and figure of which agree with *B. lagenaria*. Kiener (1834) figured what he referred to as varieties of *Purpura lagenaria* (his figs 94a and 94b), but these resemble *Nucella dubia*. His description and figures of *Purpura limbosa* are of *B. lagenaria*. Under *Purpura lagenaria*, Deshayes (1844) commented that this is not

Purpura but a *Buccinum*, and that Duclos's (1832) *Purpura cucurbita* is the same, but that Duclos's *Purpura lagenaria* is a *Purpura*.

Orr (1956) and Barnard (1959) synonymised *Buccinum violaceum* with *Burnupena cincta* and *B. catarrhacta* respectively. Although the type specimen of *Buccinum violaceum* is small and rather worn (Fig. 24), we attribute it to *B. lagenaria*. Quoy & Gaimard's (1832) illustrations of *Buccinum violaceum* do not resemble the type specimen deposited in MNHN, but their figures have been repeated in subsequent works (e.g. Kiener 1834; Tryon 1881). Quoy & Gaimard's figures also show a live snail, probably drawn by the ship's artist from a live specimen during the voyage.



Figs 23–24. 23. Type specimen of *Purpura lagenaria* Lamarck, 1822, 34.1 mm (MHNG 1101/64/1: syntype). 24. Type specimen of *Buccinum violaceum* Quoy & Gaimard, 1832: 25.2 mm (MNHN: syntype)

Burnupena lagenaria is common to abundant throughout most of its range, and is found in the mid- to high-intertidal zone in pools and exposed habitats. This species not only has the widest distribution, but also exhibits greater variation in shell form and coloration (Figs 15–22) than the other species in the genus. In terms of shell form, populations on the west and east coasts tend to be squat and have shorter spires and larger apertures (Figs 17–19), whilst those on the south coast are generally less squat with slightly longer spires and shorter apertures (Figs 15–16). The population from Kommetjie (Figs 21–22) is an exception, and resembles the south coast populations. The west and east coast populations also tend to have smoother shells, and a higher proportion of shells in which the aperture is plicate internally. In terms of shell colour, the east coast populations are generally dark with no pattern, as are some of the west coast populations. The south coast populations usually exhibit alternating dark and light dashes to a greater or lesser extent. The west coast populations are more variable, with some populations being mostly dark (for example Blouberg), whilst others show varying degrees of axial streaking.

Burnupena lagenaria has most often been confused with *B. catarrhacta* and *B. cincta*. The character states that distinguish it from these species have already been discussed under the remarks relating to them.

Burnupena papyracea (Bruguière, 1789)

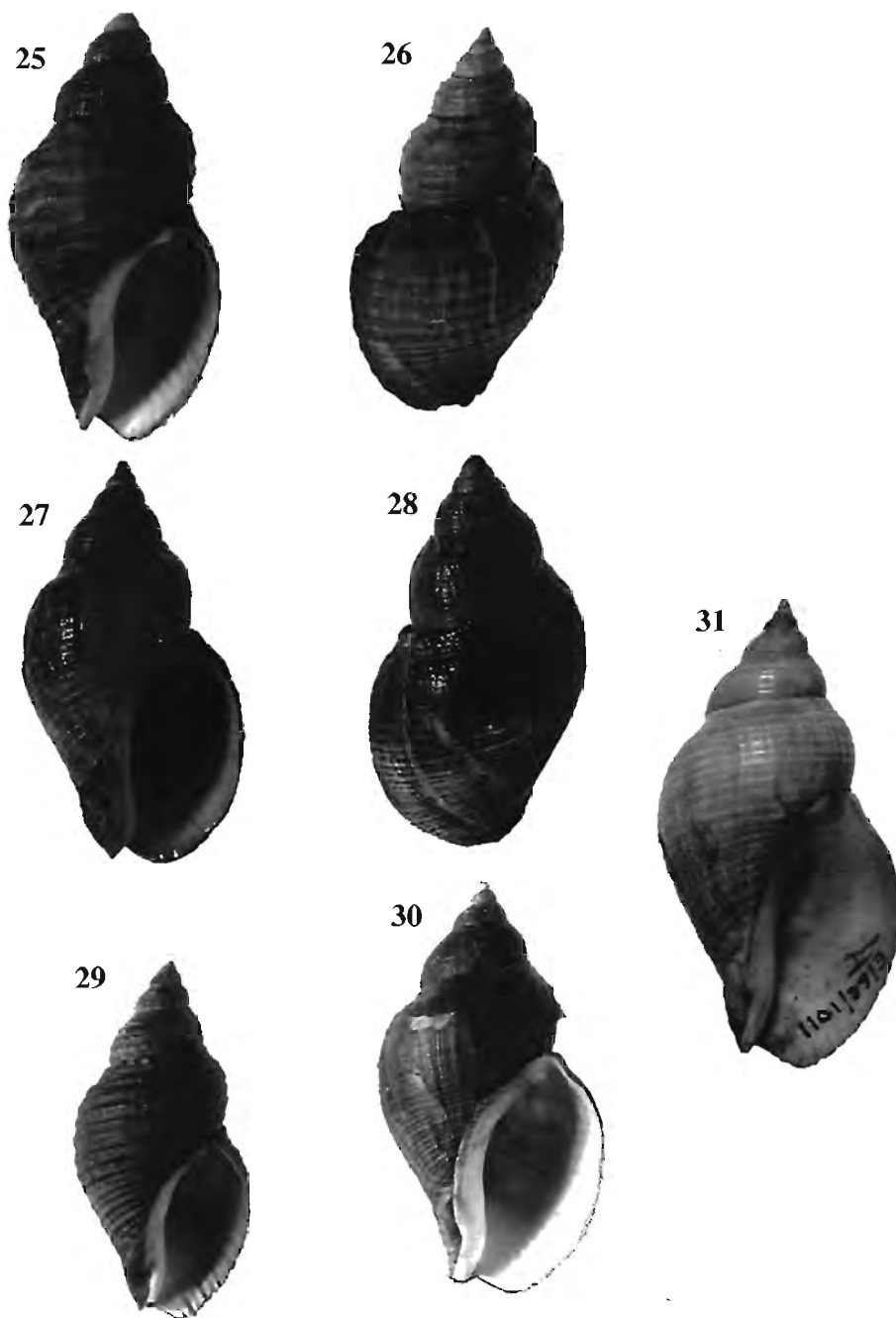
Figs 2d, 25–31, 32, 34, 36

- Buccinum papyraceum* Bruguière, 1789: 260 (type figured in Chemnitz 1780: pl. 126, fig. 1212); Lamarck, 1816: pl. 400, fig. 3a,b; Dillwyn, 1817: 634; Lamarck, 1822: 264; Kiener, 1834: 8, pl. 4, fig. 10; Deshayes, 1844: 156; Reeve, 1846, pl. 4, fig. 24.
- Buccinum anglicum* Gmelin, 1791: 3494.
- Buccinum britannicum* Röding, 1798: 113.
- Buccinum norvegicum* Lamarck 1816: pl. 339, figs 5a–b.
- Buccinum anglicanum* Lamarck, 1822: 264; Kiener, 1834: 7, pl. 4, fig. 9; Deshayes, 1844: 156; Reeve, 1846, pl. 4, fig. 23.
- Buccinum intinctum* Reeve, 1846, pl. 5, fig. 32; Krauss, 1848: 120; 1852: 36; Küster, 1858: 84, pl. 13, fig. 12, pl. 15, figs 3–4.
- Cominella (Cominella) papyracea*; Adams & Adams, 1853: 110.
- Cominella (Amphissa) intincta*; Adams & Adams, 1853: 111.
- Buccinum (Amphissa) intinctum*; Chenu, 1859: 158, fig. 738.
- Cominella porcata* var. *anglicana*; Kobelt, 1878: 231.
- Cominella papyracea*; Kobelt, 1878: 232; Tryon, 1881: 202, pl. 80, figs 401, 402 = *C. intincta*; Sowerby, 1892: 10; Bartsch, 1915: 48; Tomlin, 1922: 260; Turton, 1932: 52; Stephenson, 1948: 273.
- Cominella porcata*; Tryon, 1881: 202, *partim*, pl. 80, fig. 394 = *C. anglicana*, *non* figs 392, 393, 395, 396, 399, 404.
- Cominella anglicana*; Bartsch, 1915: 48.
- Burnupena papyracea*; Peile, 1939: 270; Barnard, 1959: 163; Kilburn, 1972: 415; Day, 1974: 166, fig.; Kilburn & Rippey, 1982: 94, pl. 21, fig. 11; Branch *et al.*, 1994: 162, fig. 76.5; Steyn & Lussi 1998: 110, fig. 433.
- Burnupena papyracea papyracea*; Orr, 1956: 252, *partim*, pl. 19, fig. 2, *non* figs 1,3–4 (shell), text fig. 1d,e (radula); Kensley, 1973: 152, fig. 554; Richards, 1981: 59, pl. 32, fig. 261.

Diagnosis: Spire moderately high, angle usually 60–70°. Shell width approximately half shell length. Aperture slightly longer than spire. Periphery of body whorl situated approximately half way up shell. Sculptured by either (a) weak to fairly strong spiral ribs, typically between 10 and 14 on body whorl, with fine spiral striae on and inbetween ribs, occasionally with deeper spiral striae on the rib, or (b) by numerous fine spiral striae throughout. Whorls with slight to no depression below suture; upper whorls typically bulging outwards and convex in profile, sometimes with deep sutures. Aperture usually plicate internally, occasionally smooth internally but crenulated at edge. Pale brown parietal scar usually present, sometimes absent. Periostracum thin, papery, brownish-yellow. Shell colour reddish-brown to brown to pale brown, sometimes mottled, sometimes with pale whitish-brown spiral bands present on part or entire shell, but most noticeable on body whorl. Aperture usually white, sometimes light mauve-brown. Live specimens covered by the bryozoan *Alcyonidium nodosum*. Proboscis flesh coloured. Maximum shell length 58 mm.

Distribution: From Lüderitz (Namibia) on the west coast, extending to Transkei on the south coast (Fig. 2d), where it is uncommon.

Material examined: Lüderitz (SAM 31261, SAM A33405, UCT, YD); Buffels River (UCT); Hondeklip (UCT); Paternoster (ANSP 196303); Marcus Island (YD); Langebaan Lagoon (UCT): Dassen Island (SAM 6879, SAM 6880); Blouberg (SAM



Figs 25–31. *Burnupena papyracea* from (25) A-Frame: 47.6 x 23.4 mm and (26) 44.2 x 22.4 mm, (27) Marcus Island: 45.2 x 24.2 mm and (28) 45.7 x 24.5 mm, (29) Pringle Bay: 41.9 x 20.8 mm and (30) Marcus Island: 48.5 x 26.3 mm, (31) Type specimen of *Buccinum papyraceum* Bruguière, 1789, 49.5 x 25.0 mm (MHNG 1101/89/3: syntype). Specimens 29–30 illustrate the differences in ribbing between the False Bay and west coast individuals.

A49964, YD); Three Anchor Bay (SAM A4744); Sea Point (SAM 2609, ANSP 196301); Bakoven (YD); Llandudno (YD); Platboom (ANSP 196300); Cape of Good Hope (BMNH 1564); False Bay: Simonstown (SAM 4749, ANSP 196200), St. James (SAM A36384), Muizenberg (SAM A4936); Castle Rock (YD), A-Frame (YD), Pringle Bay (YD); Still Bay (SAM A30981); Mossel Bay (SAM 2435); Port St. Johns (SAM 2504, SAM 2505).

Type material: *Buccinum papyraceum* Bruguière, 1789 (MHNG 1101/89 – seen from photographs): three specimens, with two probable syntypes (see remarks below), one of which (Fig. 31) matches the description given by Bruguière, as well as the figure in Lamarck, 1816 (his pl. 400, fig. 3a); locality given as Europe, but certainly incorrect.

Remarks: This species was first described and figured by Chemnitz in 1780, who named it *Buccinum anglicanum elongatum*. As noted above regarding the works of Chemnitz, the name is invalid, although a number of subsequent authors used the name '*anglicanum*' or a variation of it. Bruguière (1789) described this species from a shell in Lamarck's collection. The MHNG has a lot of three specimens of this species, which are probably from the Lamarck collection, although only two of them are original syntypes, with the third specimen probably added later on (Y. Finet, *pers. comm.*). Tryon (1881, fig. 394) regarded *Cominella anglicana* as a synonym of *Cominella porcata*.

This species was neglected by Cooke (1917) and Iredale (1918), and first mention of it belonging to *Burnupena* came from a radula study by Peile (1939) more than 20 years later.

Orr (1956) figured four specimens which she referred to as *B. papyracea papyracea*. However, only her figure 2 is this species. The other figures are as follows: (1) is *B. limbosa*, (3) is *B. lagenaria* and (4) is *B. rotunda*.

Burnupena papyracea is a relatively common species and occurs in deep pools in the low intertidal zone or subtidally in boulder-strewn habitats. Together with *B. pubescens* and the new species described below as *B. denseliriata*, it is covered by a bryozoan (which has only been identified with certainty as *Alcyonidium nodosum* in *B. papyracea*), and positive identification of these three species of *Burnupena* almost always necessitates the removal of the bryozoan. All three species co-occur in False Bay, often in mixed populations. They are genetically distinct, even in areas where they are sympatric, justifying their separation as valid species (Dempster 1995a). Morphologically, *B. papyracea* can usually be distinguished from both of the other species by the lack of axial ridges on the spire and the convex profile of the collective whorls (Figs 32–36). However, in some specimens of *B. pubescens* and *B. denseliriata* the axial ridges are not obvious, making identification more difficult (e.g. Fig. 38). Specimens of *B. papyracea* never possess alternating dark and pale dashes, which are commonly seen in specimens of *B. pubescens* and *B. denseliriata*. *B. papyracea* can also be distinguished from *B. denseliriata* by the number of spiral ribs or ridges on the body whorl, with *B. papyracea* typically having between 10 and 14, whereas *B. denseliriata* has more than 14.

Four specimens from Muizenberg (grouped as a single lot, SAM A4936) were identified by Barnard (1959) as varieties of *B. pubescens*. He noted that only the early whorls were cancellate, with nodules on the later whorls obsolete. Two of these

specimens are, however, attributable to *B. papyracea*, the other two to *B. denselirata* (see below).

Burnupena pubescens (Küster, 1858)

Figs 2e, 33, 35, 37–40

- Buccinum tigrinum* (non Gmelin, 1791) Kiener, 1834: 27, pl. 10, fig. 32; Krauss, 1848: 120; Küster, 1858: 80, pl. 14, fig. 11, pl. 15, fig. 5.
Cominella (*Cominella*) *tigrina*; Adams & Adams, 1853: 110.
Buccinum pubescens Küster, 1858: 73, pl. 13, figs 8–9.
Buccinum biserialis Küster, 1858: 80, pl. 14, fig. 12.
 ?*Buccinum robustum* Küster, 1858: 81, pl. 14, fig. 13.
Cominella porcata var. *pubescens*; Kobelt, 1878: 231.
Cominella porcata var. *tigrina*; Kobelt, 1878: 231; Tryon, 1881: 202, pl. 80, figs 395 = *C. pubescens*, 396, 399 = *C. robusta*, 404 = *C. biserialis*.
 ?*Cominella papyracea* var. *robusta*; Kobelt, 1878: 232.
Cominella biserialis; Kobelt, 1878: 232; Bartsch, 1915: 47; Turton, 1932: 51.
 ?*Cominella semisulcata* Sowerby, 1892: 10, pl. 1, fig. 7.
Cominella tigrina; Sowerby, 1892: 11; Bartsch, 1915: 47; non Cooke, 1917: 229, fig. 12 (radula); Turton, 1932: 51; Stephenson, 1948: 273.
Cominella translucida Turton, 1932: 51, pl. 12, fig. 379.
Afrocominella tigrina; Iredale, 1918: 34; Tomlin, 1926: 290.
 ?*Cominella robusta*; Turton, 1932: 51.
Burnupena tigrina; Peile, 1938: 97, fig. 32 (radula); Barnard, 1959: 166, fig. 32f.
Afrocominella tigrinus; Barnard, 1951: 69.
Burnupena papyracea tigrina; Orr, 1956: 255, pl. 19, figs 7–8 (shell), text fig. 1a (radula); Kensley, 1973: 152, fig. 555.
Burnupena pubescens; Kilburn, 1972: 415; Richards, 1981: 60, pl. 32, fig. 265; Kilburn & Rippey, 1982: 94, pl. 21, fig. 14; Branch *et al.*, 1994: 162, fig. 76.6; Steyn & Lussi, 1998: 110, figs 434, 436 (juv. as *Cominella dunkeri*).

Diagnosis: Spire moderately high, angle usually 50–60°. Shell width approximately half shell length. Aperture slightly longer than spire. Periphery of body whorl situated approximately half way up shell. Sculpture usually weak to fairly strong spiral ribs, often nodulate, early whorls cancellate. Typically between 10 and 14 ribs on body whorl, with fine spiral striae on and between ribs. Whorls slightly to moderately depressed below suture; profile of upper whorls slightly convex. Aperture usually plicate internally. Pale brown parietal scar usually present, sometimes absent. Periostracum thin, papery brownish-yellow. Shell colour yellowish-brown to reddish-brown occasionally pale brown, sometimes with pale whitish-brown spiral bands on body whorl; raised spiral ribs usually with alternating dark brown and pale whitish-brown dashes, most prominent on upper half of body whorl and on spire, giving a flecked or axially flamed appearance; this pattern is most evident in beach-worn specimens. Aperture white to light mauve-brown. Live specimens covered by a bryozoan, possibly *Alcyonidium nodosum*. Proboscis flesh coloured. Maximum shell length 41 mm.

Distribution: False Bay to KwaZulu-Natal, and sporadically on the west coast as far as Saldanha Bay (Fig. 2e).

Material examined: Saldanha Bay (UCT); Dassen Island (SAM 6886); False Bay: False Bay (SAM A3532, SAM A4743, SAM A36385), Buffels Bay (ANSP 196299), Castle Rock (YD), A-Frame (YD), Kalk Bay (SAM 4699, SAM 6543), Strandfontein (SAM A49963) and Rooiels (YD); Hermanus (ANSP 196202); Still Bay (SAM A30978); Mossel Bay (SAM 2435, SAM A4735, SAM A30976, SAM A49967,

ANSP 196293); St. Francis Bay (SAM A30980); Jeffrey's Bay (SAM A30977, SAM A49968, SAM A51345); Port Elizabeth (collected for YD by B. Hayes); East London (SAM A4734, SAM A49966); Bonza Bay (SAM A39251); Gonubie (SAM A39252); Port St. Johns (SAM 2532, SAM 11353); Mbotyi (SAM A51403); Durban (SAM 2673).

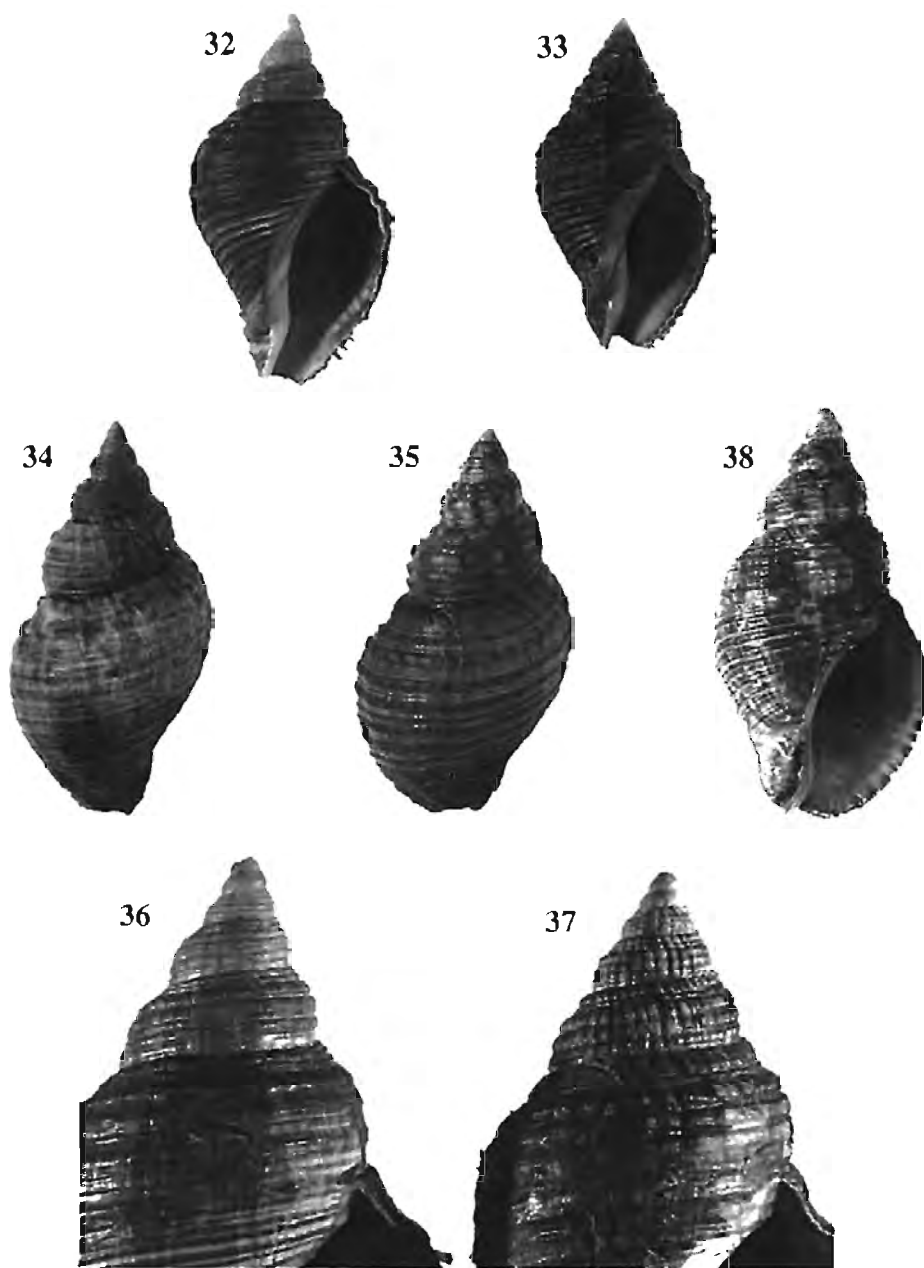
Type material: *Buccinum pubescens* Küster, 1858: the depository of Küster's types is uncertain and they are presumed lost. *Cominella translucida* Turton, 1932: holotype in OXUM.

Remarks: Krauss (1848) commented that the name *Buccinum tigrinum* had been given to a completely different shell by Gmelin and that this name cannot be applied to any *Burnupena* species. However, it was only changed to *Burnupena pubescens* much later by Kilburn (1972). Küster (1858) erected the name *Buccinum pubescens* for a shell which he regarded as differing from *Buccinum tigrinum* in its proportions and the number of spiral cords.

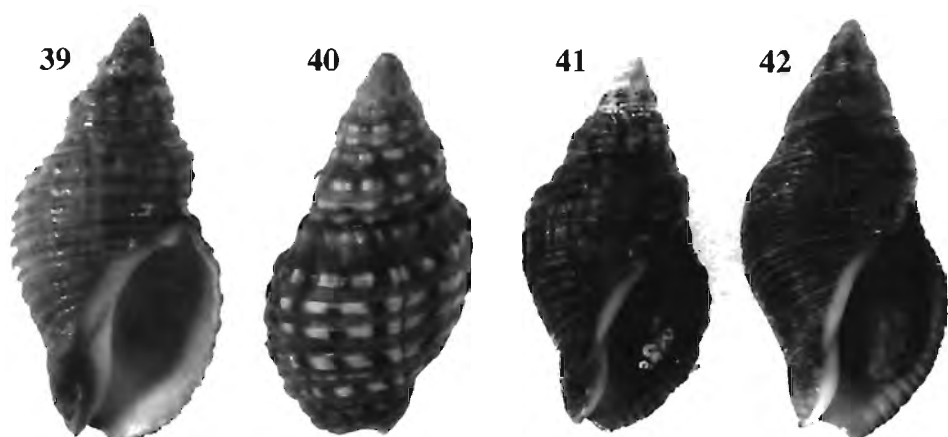
Küster's (1858) *Buccinum robustum* is problematical; it has been synonymised with *Cominella tigrina* by Tryon (1881), and with *Burnupena papyracea papyracea* by Orr (1956), but Turton (1932) retained it as a separate species. We provisionally synonymise it with *Burnupena pubescens*, in that it appears to have nodulous spiral cords, a character state of this species. However, these nodulous cords (Küster 1858, pl. 14, fig. 13) are restricted to the area just below the suture, and do not occur elsewhere on the spire. Also, *B. robustum* appears to have a large number of weak spiral ribs, more than is usual for *B. pubescens*. Since Küster's types are presumed lost, it is not possible to examine this nominal species. Küster recorded the locality as the Cape and KwaZulu-Natal coasts, but if this species is not the same as *B. pubescens*, nor *Burnupena denselirata*, to which it also bears some resemblance (see comments below), then it must be regarded as a species *incertae sedis*.

Iredale (1918) assigned *Cominella tigrina* to *Afrocominella* based on the results of a study by Cooke (1917) of the radulae of the genus *Cominella*. However, in a later study, Peile (1938) found that the slide seen by Cooke had been incorrectly labelled, and that the radula figured by Cooke as '*C. tigrina*' was indistinguishable from *Afrocominella elongata* (Dunker). Peile's study of the radula confirmed that this species is correctly attributable to *Burnupena*.

The identity of Sowerby's (1892) *Cominella semisulcata* is uncertain. Orr (1956) regarded it as a synonym of *B. cincta*, Barnard (1959) placed it with *B. pubescens*, and Kilburn & Rippey (1982) discuss it under *B. cincta*, but comment that its relationship with *B. pubescens* needs investigation. Examination of two lots in the SAM (A3178 & A30980), initially identified as *Cominella semisulcata* but subsequently changed to *C. tigrina*, lead us to conclude that this taxon is most probably a form of *B. pubescens*. All of the specimens in both lots are beach worn. The shells are rather elongate with high spires and are smooth, but shows traces of axial ridges on the top whorls. Barnard commented that Sowerby's figure was not good because the subsutural groove was drawn too deep. A living specimen collected at Port Elizabeth (SAM A51966), does not help, since although it is not worn, the top whorls are obscured by a hard coralline alga. The shell is slender, with an acute spire. The body whorl is brown and the aperture pale.



Figs 32-38. *Burnupena papyracea* and *B. pubescens*, illustrating differences between the two species: (32 & 34) *B. papyracea* and (33 & 35) *B. pubescens*, all from A-Frame; (36) *B. papyracea* and (37) *B. pubescens*: details of spire to illustrate differences in sculpture; (38) *B. pubescens* from Castle Rock, showing a barely cancellate spire; (32) 27.2 x 15.0 mm; (33) 24.3 x 13.4 mm; (34) 38.7 x 19.7 mm; (35) 38.1 x 19.8 mm; (38) 31.7 x 16.9 mm.



Figs 39–42. *Burnupena pubescens* and *B. denseliriata* sp. n.: (39) *B. pubescens* from A-Frame, 38.1 x 19.8 mm (same specimen as Fig. 35), (40) *B. pubescens* from East London, 36.0 x 18.7 mm (SAM A49966); (41) *B. pubescens* from Castle Rock 29.6 x 15.2 mm; (42) *B. denseliriata* sp. n. from Miller's Point, 33.2 x 16.4 mm (SAM A51965: paratype).

Burnupena pubescens occurs subtidally in boulder-strewn habitats, and is not as common as *B. papyracea*. As noted above, the bryozoan covering needs to be removed from living specimens before they can be identified. *B. pubescens* can be confused with both *B. papyracea* and *B. denseliriata*, and differences between it and *B. papyracea* have been discussed above. *B. pubescens* differs from *B. denseliriata* in the number of spiral ribs or ridges on the body whorl – typically 10 to 14 in *B. pubescens* and more than 14 in *B. denseliriata*, and in the presence of nodules in *B. pubescens* on the shell other than on the top whorls (Figs 39–42). The presence of axial flames on the body whorl is common in *B. pubescens* but has not been observed in *B. denseliriata*.

***Burnupena rotunda* sp. n.**

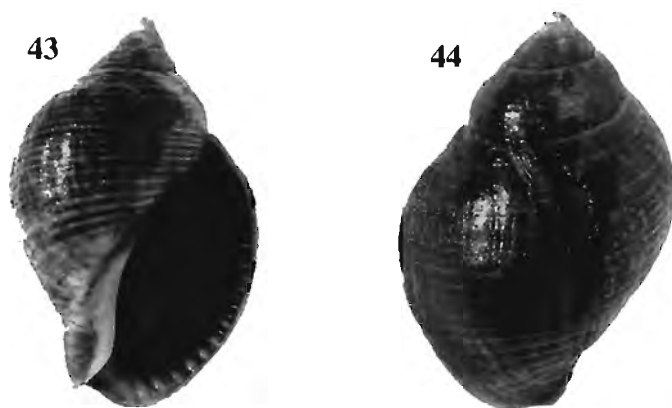
Figs 2f, 43–44

Burnupena papyracea papyracea (non Bruguière); Orr, 1956: 252, *partim*, pl. 19, fig. 4, non figs 1–3.

Burnupena sp. Branch *et al.*, 1994: 162, fig. 76.4.

Etymology: *rotunda* – referring to the rotund shape of the shell.

Diagnosis: Shell squat with low spire, angle usually 70–80°. Shell width more than half shell length. Aperture approximately twice as long as spire. Periphery of body whorl situated closer to apex than to base. Sculptured by numerous fine spiral striae. Whorls with slight to no depression below suture; profile of upper whorls straight. Shell robust. Outer lip thick, aperture usually plicate internally. Dark brown parietal scar usually present. Periostracum thick, fibrous, olive-brown. Shell colour dark bluish-brown, usually with thin pale bluish-grey spiral bands, most visible on body whorl; shell sometimes worn, upper whorls usually worn. Aperture sometimes pale whitish to mauve-brown, sometimes dark brownish-violet. Proboscis flesh coloured. Maximum shell length 46 mm.



Figs 43–44. *Burnupena rotunda* sp. n. from Groen River: (43) 32.0 x 20.4 mm (SAM A51961: Holotype); (44) 35.2 x 22.8 mm (SAM A51962: paratype).

Description of holotype: Shell sculptured by numerous fine spiral striae. Whorl hardly depressed below suture. Outer lip crenulated at edge, aperture plicate internally. Dark black brown parietal scar present. Periostracum mostly worn, but at outer edge of aperture thick, fibrous olive green-brown. Shell with alternating dark blue-brown and pale blue grey spiral bands. Aperture dark brownish-violet, whitish at anterior tip.

Dimensions: Shell length 32.0 mm; shell width 20.4 mm; aperture length 23.1 mm; aperture width 10.6 mm; spire length 11.6 mm.

Distribution: West coast from Lüderitz (Namibia) southwards, and extending around Cape Point to Simonstown (Fig. 2f).

Material examined: Lüderitz (SAM A30521, SAM A30530, YD); Orange River mouth (SAM A29857); Groen River (YD); Lamberts Bay (SAM A30986); Paternoster (ANSP 196303); Marcus Island (YD); Bakoven (YD); Oudekraal (SAM A36383); Cape of Good Hope (BMNH 1840.9.20.26); Simonstown (SAM 4754).

Type material: **Holotype**, SAM A51961, living, low intertidal zone, rocky shore, Groen River on the west coast of South Africa, collected by G. M. Branch. **Paratypes 1–15**, SAM A51962, same data; **Paratypes 16–30**, NM V958/T1330, same data.

Remarks: *Burnupena rotunda* inhabits the low intertidal to subtidal zone. In terms of shell shape, it is most similar to *B. lagenaria*, both species being typically squat, with obtuse spires and relatively large apertures. They do differ in the degree of depression below the suture, with *B. rotunda* hardly depressed, and *B. lagenaria* markedly so; internally the aperture of *B. rotunda* is plicate whilst that of *B. lagenaria* is not; the shell colour also differs, with *B. rotunda* dark blue-brown with pale spiral bands, and *B. lagenaria* flecked or axially flamed, sometimes brown without flecks, although both species are often worn.

This species occurs in a number of museum collections, but has variously been identified as *B. limbosa* (SAM 4754, SAM A29857, SAM A30986, SAM A36383,

BMNH 1840.9.20.26), *B. catarrhacta* (SAM A30521, SAM A30530) or *B. papyracea* (ANSP 196303). However, it is distinct, both morphologically and genetically (Dempster 1995a). Character states that distinguish it from *B. c. limbosa* have been discussed above. *B. rotunda* differs from *B. catarrhacta* in a number of respects: it has a totally different shape, being low-spired and squat; the relative size of the aperture is much larger; there is little or no depression below the suture; the aperture is usually plicate internally; the shell is thick and robust; the periostracum is thick and fibrous; the shell is patterned with spiral bands and not axial flames. The only case in which *B. rotunda* has been identified as *B. papyracea* was that of Orr (1956 – ANSP 196303), who figured a specimen of this species as one of her examples of *B. papyracea* (her Pl. 19, fig. 4). However, she synonymised *B. limbosa* with *B. papyracea*, so it is not clear to which species she initially attributed this specimen. *B. rotunda* can be distinguished from *B. papyracea* by the following characters: (1) the overall shape of the shell of *B. rotunda* is squat with a low spire, whilst that of *B. papyracea* is more slender; (2) the profile of the upper whorls are convex in *B. papyracea*, but not so in *B. rotunda*; (3) the periostracum in *B. papyracea* is papery, but is fibrous in *B. rotunda*; (4) the shell colour in *B. rotunda* is dark with pale spiral bands, but is reddish- to pale brown in *B. papyracea*.

***Burnupena denseliriata* sp. n.**

Figs 42, 45–46

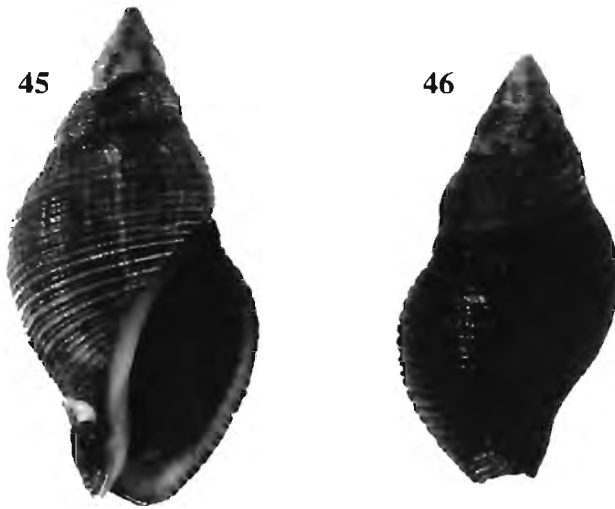
?*Buccinum robustum* Küster, 1858: 81, pl. 14, fig. 13.

Burnupena tigrina; Barnard, 1959: 168, *partim* (reference to two specimens in lot SAM A4936).

Etymology: *denseliriata* – referring to the dense, clearly defined, fine spiral lirae.

Diagnosis: Spire moderately high, angle usually 50–60°. Shell width approximately half shell length. Aperture only slightly longer than spire. Periphery of body whorl situated slightly closer to base of shell than to apex. Sculptured by numerous, weak, spiral ridges, often occurring in pairs on lower half of body whorl, sometimes with only an incised groove separating paired ribs when they lie side by side. Only the early whorls cancellate, and then weakly so. Whorls slightly depressed below suture; profile of upper whorls straight. Aperture usually plicate internally. Pale brown parietal scar usually present, sometimes absent. Periostracum thin, fibrous, brownish-yellow. Shell colour orange-brown to reddish-brown; upper whorls with alternating dark (same colour as the shell) and pale yellowish-brown dashes, giving an axially striped appearance; the body whorl has no axial stripes but the spiral threads between the ridges are usually paler, especially on lower half of body whorl. Aperture white to light mauve-brown. Live specimens are covered by a bryozoan, possibly *Alcyonidium nodosum*. Proboscis flesh coloured. Maximum shell length 47 mm.

Description of holotype: Sculptured by numerous weak spiral ridges which occur in pairs. Top whorls weakly cancellate. Depression below the suture moderate. Outer lip thin, aperture plicate internally. Parietal scar absent. Periostracum thin fibrous yellowish-brown, present only on lower half of body whorl. Shell orange-brown, with pale brown to whitish spiral bands between ridges. Upper whorls with alternating pale yellowish-brown and orange brown dashes, with the latter aligning to give a streaky appearance. Aperture pale mauve-brown.



Figs 45–46. *Burnupena denseliriata* sp. n. from: (45) A-Frame 35.5 x 18.2 mm (SAM A51963: Holotype); (46) Miller's Point 33.2 x 16.4 mm (SAM A51965: paratype, same specimen as Fig. 42).

Dimensions: Shell length 35.5 mm; shell width 18.2 mm; aperture length 21.2 mm; aperture width 8.6 mm; spire length 17.8 mm.

Distribution: Known only from False Bay.

Material examined: Muizenberg (SAM A4936); Castle Rock (YD); Miller's Point (YD); A-Frame (YD); Rooiels (YD).

Type material: **Holotype**, SAM A51963, living, subtidal 5–10 m, boulder strewn, A-Frame, False Bay, collected by YD. **Paratype 1**, SAM A51964, same data; **Paratypes 2–4**, SAM A51965, living, subtidal 5–10 m, boulder strewn, Miller's Point, False Bay, collected by YD. **Paratypes 5–6**, NM V957/T1329, same data.

Remarks: As noted above in connection with *B. pubescens*, the position of Küster's *Buccinum robustum* is unclear. Although we have provisionally synonymised it with *B. pubescens*, it does bear some resemblance to *B. denseliriata* in having numerous weak spiral ribs. However, although *B. denseliriata* does have a weakly cancellate spire, the distinct nodulous cords seen in the figure of *Buccinum robustum* are not present in *B. denseliriata*.

As noted under *B. papyracea*, a lot of four specimens from Muizenberg (SAM A4936) was identified by Barnard (1959) as varieties of *B. pubescens*. Two were attributable to *B. papyracea*; the other two were described as having only the early whorls cancellate, and the major costae as scarcely stronger than lirae, both of which are character states of *B. denseliriata*.

This species occurs subtidally in boulder-strewn habitats, and is very rare. As in the case of both *B. papyracea* and *B. pubescens*, the shell is covered by a bryozoan which must be removed from living specimens before they can be identified. It was originally confused with *B. pubescens* due to the presence of the weakly cancellate spire, but they were found to be genetically distinct (Dempster 1995a). Referral back

to the shells of specimens used for electrophoresis revealed that there were also morphological differences between these two species, which have been noted above under the comments on *B. pubescens*. The differences between *B. denseliriata* and *B. papyracea* have also been discussed above under the latter species.

DISCUSSION

The overall conclusion drawn from morphometric analyses (Dempster 1995a) was that the degree of intraspecific morphological variation within *Burnupena* species is relatively large when compared with the variation within the genus as a whole. Whereas some species can be identified with little difficulty, there will always be some individuals that will be more similar morphometrically to another species; between such species there is a continuum of overlapping forms, with the individuals at each extreme being more or less distinctive. Discriminant analyses indicated that about 94 % of the individuals examined could be correctly identified, indicating a slightly lower diagnostic value for morphological variation when compared to genetic variation (above 95 %), due to the greater susceptibility of the former to environmental conditions (Dempster 1995a).

An examination of the radulae of all the species revealed that the radula is of little or no value in distinguishing between them (Dempster 1995a). Although some differences could be detected, these were not consistent, both within and between species. However, the radula is diagnostic for the genus, as it clearly differs from that of its close relative *Afrocominella*.

Electrophoretic analyses revealed that all the species recognised in this paper are genetically well differentiated (Dempster 1995a). Using a combination of loci and species-specific alleles, all the individuals of each of the species described here could be identified. At the one end of the scale, *B. catarrhacta* was so well differentiated from the other species that it might justifiably be assigned to a separate genus. However, in the case of *B. lagenaria* (previously considered a valid species), some populations were more different from their conspecifics elsewhere than they were from *B. cincta*, and it was not always possible to unambiguously distinguish the two taxa, although the probability of making the correct assignment was high (above 95 %). Thus, although usually genetically distinct, *B. cincta* and *B. lagenaria* exhibited much lower levels of differentiation relative to all the other species. Indeed, the genetic distances between the populations of these two taxa were so low as to fall within the range expected between conspecific populations. Consequently, we propose that they are subspecies.

In summary, morphometric and electrophoretic data allow the recognition of seven species, one being divisible into two subspecies. This paper provides descriptions of these and a key to the species. In conjunction with remarks about the characters (or suites of characters) which can be used to distinguish between morphologically similar species, this should enable one to correctly identify the majority of the individuals belonging to *Burnupena*. However, within species, the form and colour of the shell can be influenced by local environmental conditions, giving rise to differences between local populations. Unquestionably, there will always be some

TABLE 1

Summary of the character states of the species of *Burnupena*. Ratios are given as mean (and range). Shell lengths (mm) indicate the size ranges recorded.

Character	<i>B. catarrhacta</i>	<i>B. c. cincta</i>	<i>B. c. limbosa</i>	<i>B. lagenaria</i>	<i>B. papyracea</i>	<i>B. pubescens</i>	<i>B. rotunda</i>	<i>B. denseliriata</i>
Spire height/ shell length	Moderate 0.47 (0.43–0.51)	Moderate 0.46 (0.38–0.51)	Moderate-high 0.46 (0.39–0.55)	Low 0.40 (0.30–0.49)	High 0.50 (0.45–0.59)	Moderate-high 0.48 (0.44–0.52)	Low 0.43 (0.37–0.50)	Moderate-high 0.48 (0.44–0.52)
Shell width/ shell length	Approx. half 0.53 (0.49–0.57)	Approx. half 0.53 (0.48–0.60)	Slightly > half 0.56 (0.48–0.63)	More than half 0.60 (0.52–0.71)	Approx. half 0.52 (0.43–0.60)	Approx. half 0.52 (0.48–0.58)	More than half 0.61 (0.56–0.69)	Approx. half 0.52 (0.49–0.55)
Spire height/ aperture length	Slightly shorter 0.83 (0.68–0.95)	Slightly shorter 0.77 (0.55–0.97)	Slightly shorter 0.76 (0.47–1.08)	About half 0.66 (0.37–0.82)	Shorter to equal 0.91 (0.66–1.23)	Slightly shorter 0.86 (0.74–1.03)	About half 0.64 (0.50–0.89)	Slightly shorter 0.83 (0.70–0.99)
Sculpture	Numerous spiral striae	4–9 strong spiral ribs	Numerous spiral striae	4–9 weak spiral ribs, or spiral striae	10–14 weak to strong spiral ribs, or fine spiral striae; no cancellation	10–14 weak to strong spiral ribs, often nodulate. Early whorls cancellate	Numerous spiral striae	> 14 weak spiral ridges, often paired; early whorls weakly cancellate
Depression below suture	Moderate	Moderate to strong	Slight to moderate	Moderate to strong	Slight to none	Slight to moderate	Slight to none	Slight
Interior of aperture	Smooth, crenulate at margin	Smooth, undulate at margin	Plicate	Smooth, crenulate at margin	Plicate	Plicate	Plicate	Plicate
Parietal scar	Dark	Pale	Pale	Dark	Pale	Pale	Dark	Pale
Periostracum	Thin, yellow- brown	Thick, fibrous greenish-brown	Thick, fibrous brown	Thick, fibrous greenish- brown	Thin, papery, yellow-brown	Thin, papery, yellow-brown	Thick, fibrous greenish-brown	Thin, yellow- brown
Shell colour	Greenish to yellow-brown with darker axial flames	Dark brown, occasionally with a few pale flecks	Dark brown	Yellow-brown with dark and pale dashes, or plain brown	Reddish-brown to pale brown	Yellowish- to reddish-brown, to pale brown, often flecked	Dark bluish- brown with pale spiral bands	Orange- to reddish-brown, early whorls flecked
Aperture colour	Dark brownish- violet	Pale mauve- brown to violet	White to pale mauve-brown	Dark brownish- violet	White to pale mauve-brown	White to pale mauve-brown	Pale white-mauve, or dark brown-	White to pale mauve-brown
Bryozoan coating	No	No	No	No	Yes	Yes	No	Yes
Proboscis	Black	Flesh-coloured	Flesh-coloured	Flesh-coloured	Flesh-coloured	Flesh-coloured	Flesh-coloured	Flesh-coloured
Shell length	21–35	32–64	30–60	19–45	23–58	21–41	27–46	34–46
Profile of upper whorls	Slightly convex	Straight to stepped	Slightly convex	Straight to stepped	Distinctly convex	Slightly convex	Straight	Straight

individuals that will either be incorrectly identified, or will not be identified with any certainty.

To help resolve species identities, a summary of typical character states for each species of *Burnupena* is given in Table 1; the most significant of these diagnosing each of the species are as follows:

- *B. catarrhacta*: relatively high spired, with aperture about same length as spire; shell with a pattern of axial flames, dark aperture and parietal scar; proboscis black.
- *B. cincta cincta*: high spired; sculptured by four to nine strong spiral ribs.
- *B. cincta limbosa*: high spired; numerous fine spiral striae, aperture plicate internally.
- *B. lagenaria*: low spired, aperture longer than spire; squat, strongly depressed below suture.
- *B. papyracea*: high spired; profile of upper whorls distinctly convex, little to no depression below suture, periostracum papery.
- *B. pubescens*: high spired; early whorls cancellate, 10–14 spiral ribs, flecked pattern on shell.
- *B. rotunda*: low spired, squat, sculptured by numerous fine spiral striae; little to no depression below suture.
- *B. denseliriata*: high spired; early whorls weakly cancellate, more than 14 weak spiral ridges, shell with flecked pattern on upper whorls only with remainder of shell a uniform colour.

In addition to the living species of *Burnupena* recognised here, two fossil species have been described from Hondeklip on the west coast (Kensley & Pether 1986). The first of these, *B. rogersi*, was described as follows: shell plump, about 1.5 times longer than wide; profile of the early whorls evenly convex; sculptured by fine spiral bands; strongly sunken suture; inner surface of outer lip with faint ridges. Kensley & Pether noted that this species bore some resemblance to the genus *Babylonia*, but remarked that the South African species of *Babylonia* do not possess spiral sculpture. They also noted that *B. rogersi* resembled some species of *Burnupena*, especially *B. papyracea*, which does sometimes have a sunken suture. They note however, that the generic position cannot be established with certainty in the absence of the radula, soft parts and operculum. The second fossil species, *B. aestus*, was described as follows: shell elongate, slender, spire longer than aperture; profile of whorls convex with slight depression below the suture; sculptured by fine spiral lirae; inner surface of outer lip ridged. In their remarks, Kensley & Pether noted that this species most resembles *Afrocominella capensis* (Philippi) in general proportions, but lacks the axial ridges of the early whorls typical of this species. *B. aestus* is also similar to *B. papyracea*, although this species is not as slender and has fewer spiral lirae.

In conclusion, we consider that there are seven valid extant species in *Burnupena*, and this paper outlines the characteristics by which they can be identified. Several of these species would have been difficult or impossible to distinguish purely on morphological grounds, but were clearly distinct when analysed electrophoretically. Indeed, one of the new species described here (*B. denseliriata*) would almost certainly never have been detected on morphological grounds alone. The genus will always remain vexing in terms of our ability to identify some individuals, but we are

confident that the joint application of morphology and genetics resolves the taxonomy of the group.

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